Thiago Macek Gonçalves Zahn

Integração morfológica no crânio e evolução da
morfologia craniana em Feliformia (Carnivora:
Mammalia)

Skull morphological integration and evolution of skull
morphology in Feliformia (Carnivora: Mammalia)

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A quem trouxe; a quem levou;
a quem acompanhou; a quem foi;
a quem ficou; a todos que marcaram.
Este trabalho não é fruto de um. A estes muitos.

E aos carnívoros, esse grupo genial que me fez companhia durante todo o processo.
Em homenagem a alguns de seus membros menos conhecidos desse lado do Atlântico Sul, reproduzo
aqui uma lenda indiana sobre a avareza e as aparências, que tem como um de seus personagens principais
um jovem mangusto (*Urva auropunctata*).

The Loyal Mongoose

In a certain town, there was once a Brahman named *Devasharma*. His wife mothered a single son and a mongoose. And as she loved little ones, she cared for the mongoose like a son, giving him milk from her breast, and salves, and baths, and so on. But she did not trust him, for she thought: "A mongoose is a nasty kind of creature. He might hurt my boy."

One day she tucked her son in bed, took a waterjar, and said to her husband: "Now, I am going for water. You must protect the boy from the mongoose." But when she was gone, the Brahman went off himself to beg for food, leaving the house empty.

While he was gone, a black snake came from its hole and, as fate would have it, crawled toward the baby's cradle. But the mongoose, feeling him a natural enemy and fearing for the life of his baby brother, fell upon the vicious serpent halfway, battled him, tore him to bits and tossed the pieces far and wide. Then, delighted with his own heroism, he ran, blood trickling from his mouth, to meet the mother; for he wished to show what he had done.

But when the mother saw him coming, saw his bloody mouth and his excitement, she feared that the villain must have eaten her baby boy, and without thinking twice, she angrily dropped the water-jar upon him, which killed him the moment it struck. There she left him without a second thought, and hurried home, where she found the baby safe and sound, and near the cradle a great black snake, torn to bits. Overwhelmed with sorrow because she had thoughtlessly killed her benefactor, her son, she beat her head and breast.

At this moment the Brahman came home with a dish of rice gruel which he had got from someone in his begging tour, and saw his wife bitterly lamenting her son, the mongoose. "Greedy! Greedy!" she cried. "Because you did not do as I told you, you must now taste the bitterness of a son's death, the fruit of the tree of your own wickedness. Yes, this is what happens to those blinded by greed...."

.

Glück

*Solang du nach dem Glücke jagst,
Bist du nicht reif zum Glücklichen,
Und wäre alles Liebste dein.*

*Solange du um Verlorenes klagst
Und Ziele hast und rastlos bist,
Weißt du noch nicht, was Friede ist.*

*Erst wenn du jedem Wunsch entsagst,
Nicht Ziel mehr noch Begehren kennst,
Das Glück nicht mehr mit Namen nennst,*

*Dann reicht dir des Geschehens Flut
Nicht mehr ans Herz, und deine Seele ruht.*

Hermann Hesse,
Das Lied des Lebens: Die schönsten Gedichte

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Capítulo 1 - Introdução Geral

Variação morfológica, Integração e Modularidade

Varição herdável é a matéria prima para a evolução. Esta ideia - existência de variação individual transmissível entre gerações como base necessária para alterações evolutivas - já se encontrava na obra de Charles Darwin sobre a origem das espécies (Darwin, 1859), e se tornou base e guia para estudos evolutivos ainda antes da concepção e consolidação da “teoria sintética da evolução” em meados do século XX. Desde então, trabalhos diversos expandiram e definiram melhor as formas de compreender e investigar a evolução de linhagens e de caracteres entre e dentro destas linhagens, incluindo contribuições relacionadas a mecanismos de herança de características fenotípicas (genética, genética de populações e genética quantitativa, ex: Crow & Kimura, 1970; Lewontin, 1974; Nei, 1975; Falconer & McKay, 1996; Lynch & Walsh, 1997), às formas como se origina a variação dentro de uma linhagem (ex. Wagner & Altenberg, 1996; Lipson *et al.*, 2002, Beldade *et al.*, 2005) e a processos pelos quais a evolução se dá a partir de variação pré-existente – incluindo a introdução de conceitos como deriva genética (Fisher, 1922, 1930; Wright, 1931; entre outros) e evolução neutra (Kimura, 1968a, b, 1970; entre outros).

Para a morfologia e outros caracteres complexos, a variação fenotípica presente em populações naturais decorre de um processo que envolve a ação de um conjunto de genes que contribuem para a determinação do fenótipo, por meio de efeitos aditivos (efeitos médios dos alelos), de dominância (interações entre alelos de um locus) e epistáticos (interações entre loci), além de desequilíbrios de ligação (associação não-aleatória de alelos entre loci distintos) e efeitos pleiotrópicos (efeitos de um único locus sobre diversas características fenotípicas). Envolve, também, a relação entre esses determinantes genotípicos, pressões relacionadas ao desempenho funcional sob determinadas condições ambientais, bem como os legados da história evolutiva de uma linhagem, incluindo seu processo de desenvolvimento e as relações entre caracteres que ocorrem durante esta, e possivelmente ainda outros fatores adicionais (Olson & Miller, 1951, 1958, Cheverud, 1982, 1984; Falconer & Mackay, 1996, Polly, 2008). Estudos da estrutura de variação dentro e/ou entre populações já tinham presença ubíqua na literatura biológica antes mesmo que houvesse uma melhor compreensão sobre os processos de geração dessa variação, alguns deles buscando já então fazer inferências

sobre suas implicações evolutivas (ex. Lock, 1906; Stalker & Carson, 1947; Olson & Miller, 1951).

O conceito de Integração Morfológica tem sua origem mais remota no final do século XVIII, com a enunciação por Cuvier do "princípio de correlação das partes" ("o número, a direção e a forma dos ossos (...) guarda sempre uma relação necessária com todas as demais partes"). Entretanto, são os estudos da estrutura de variação de caracteres que dão ao conceito de Integração morfológica sua forma atual, em que se sabe que as relações entre partes não são "sempre necessárias" e geralmente não envolvem todas as estruturas de um organismo de forma homogênea. A integração morfológica em sua versão atual foi definida de forma explícita por Olson & Miller (1958) como a variação coordenada de caracteres devido à função ou ao desenvolvimento compartilhado - enfatizando assim a forma como conjuntos de caracteres que compartilham uma função ou uma via de desenvolvimento tendem a mostrar maior interdependência (i.e. maior correlação) em sua expressão fenotípica. A botânica russa Raissa Berg publicou na mesma época um trabalho pioneiro em que propõe um significado ecológico para os diferentes valores de correlação encontrados em medidas representando dois conjuntos de caracteres (vegetativos e reprodutivos) em diversas espécies de plantas (Berg, 1960). A autora mostra que espécies vegetais dependentes de polinização por animais apresentavam integração maior (i.e. maiores correlações) dentro de cada conjunto de caracteres, mas baixa correlação *entre* os dois conjuntos. Ela se referiu a estes conjuntos de caracteres muito integrados *internamente*, mas pouco integrados a outros conjuntos de caracteres, como "plêiades de correlação" - nome cunhado em trabalho ainda anterior sobre a correlação entre conjuntos de caracteres em rãs, realizado pelo também russo Terentjev (1931), atualmente substituído no vocabulário científico ocidental pelo termo "módulos".

A modularidade é, portanto, um conceito intimamente relacionado à integração morfológica, e pode ser compreendida como uma forma de "outro lado da moeda" da integração (Assis *et al*, 2016). Integração morfológica pode ser definida como "coesão entre caracteres resultante de interações dos processos biológicos que produzem as estruturas fenotípicas estudadas" (Klingenberg, 2008),, portanto geralmente ocorrendo entre caracteres ligados por função ou desenvolvimento. A modularidade, enquanto isso, pode ser definida como a propriedade de um conjunto de caracteres ou subunidades ("módulos") apresentarem correlações mais altas entre si que com outros conjuntos de caracteres e outras subunidades (Berg, 1960; Wagner *et al*, 2007). De certa

forma, então, ambos os conceitos lidam com o mesmo processo, mas enfatizando aspectos contrários: enquanto a integração morfológica foca-se nas associações entre os caracteres, a modularidade dá ênfase à relativa independência ou autonomia de partes de uma estrutura. Assim, o estudo dos padrões de integração em uma estrutura quase que necessariamente implica obter informações também sobre seus padrões de modularidade.

Estruturas modulares, interpretadas como resultantes de compartilhamento funcional ou de relações ontogenéticas entre seus caracteres componentes (Olson & Miller, 1958; Berg, 1960), geralmente apresentam também uma base genética compartilhada (Cheverud 1982; 1984), relacionada com o conjunto de padrões de pleiotropia e epistasia da rede genética envolvida na determinação de seus caracteres (Falconer & Mackay, 1996; Cheverud, 2004; Wagner & Zhang, 2011; Pavlicev *et al*, 2011a) e com interações epigenéticas entre caracteres (Hallgrimsson *et al*, 2009). Por esta razão, módulos tendem a evoluir como unidades integradas, o que tem importantes implicações para a evolução fenotípica (Lande, 1979; Pavlicev *et al*, 2011b).

Esta importância evolutiva poder ser compreendida tendo como base a equação multivariada de resposta à seleção (Lande, 1979 - ver **Figura 1-1**):

$$\Delta z = G \cdot \beta$$

onde Δz é um vetor com as respostas fenotípicas de cada caráter, β é um vetor com os gradientes de seleção sobre cada caráter (i.e. coeficientes de regressão parcial entre aptidão e valor fenotípico para um caráter, mantendo os outros caracteres constantes) e G é a matriz de covariância genética aditiva entre os caracteres (i.e. uma matriz representando a variação genética associada a cada caráter e as covariâncias entre caracteres). A covariação, e portanto a integração entre os caracteres, afeta assim diretamente como cada população responde às pressões seletivas.

As implicações evolutivas da integração provêm tanto dos *padrões* de integração morfológica (i.e. quais partes de uma estrutura são mais integradas) como das *magnitudes* de integração ("quanta" covariância, no geral, existe entre as partes) - Marroig *et al* (2001 - ver **Figura 1-2**). Os *padrões* de integração definem o conjunto de relações existentes entre os elementos morfológicos, reconhecíveis por exemplo por meio da análise da direção das correlações entre caracteres (Porto *et al*, 2009). A *magnitude* de integração, por outro lado, refere-se à intensidade da associação entre caracteres (Porto *et al*, 2009), ou de forma equivalente, ao nível geral de correlação de

uma distribuição multivariada de caracteres ou ao "nível de integração" de uma estrutura (Haber, 2011).

Uma vez que padrão e magnitude são aspectos complementares da integração morfológica, e portanto da estrutura das matrizes de covariância (**G** ou **P** - ver abaixo), ambos definem em conjunto as direções e intensidades das respostas de uma população a dada pressão seletiva. O padrão de integração define (por meio da estrutura de correlações entre caracteres) quais direções do espaço de caracteres têm maior variação genética aditiva disponível, afetando a direção das respostas seletivas já que estas tendem a ser enviesadas para direções com maior variação genética (LLR, ou "linhas de menor resistência evolutiva"; Schluter, 1996). Ao mesmo tempo, a magnitude de integração ("nível de integração") pode ser entendida e mensurada diretamente a partir da intensidade das correlações entre caracteres (p.ex. coeficiente médio de determinação r^2 - Van Valen, 1974) ou equivalentemente a partir da dispersão da variância contida em cada eixo de maior variação (p.ex. variância relativa dos autovalores, rVE - Van Valen, 1974; Wagner, 1984; Pavlicev *et al*, 2009a; ou coeficiente de variação dos autovalores, ICV - Shirai & Marroig, 2010). Estruturas com maior integração total têm grande parte da variação correlacionada entre diversas partes, resultando em uma redução da dimensionalidade da variação (Pavlicev *et al*, 2009a), o que se reflete em uma restrição às possíveis respostas dessa estrutura à seleção. Estruturas com magnitude de integração menor, por outro lado, têm menor limitação em suas respostas evolutivas. Colocando de outra forma, distribuições multivariadas de caracteres menos excêntricas, com variação distribuída de forma mais equitativa em todas as direções (i.e. com menor nível de integração), conseguem responder evolutivamente de forma mais alinhada a tipos distintos de seleção; por outro lado, a intensidade de suas respostas à seleção em algumas direções particulares pode ser menor (Vermeij, 1973; Hansen & Houle, 2008; Haber, 2011). Por esta razão, a magnitude de integração tem também o potencial de exercer importante influência sobre padrões macroevolutivos de evolução fenotípica (Hansen & Houle, 2008; Pavlicev *et al*, 2009a, b; Marroig *et al*, 2009; Bolstad *et al*, 2014), ainda que a relação entre as restrições microevolutivas expressas pela integração em uma espécie e seus efeitos na escala macroevolutiva de divergências entre espécies não seja direta (Bolstad *et al*, 2014).

Figura 1-1 - Representação da resposta (Δz) de duas populações hipotéticas com matrizes de covariância genética aditiva (G) distintas a uma mesma pressão seletiva (gradiente de seleção β), seguindo a equação de resposta à seleção de Lande (1979): $\Delta z = G \cdot \beta$, ilustrando implicações evolutivas da integração entre caracteres. Na situação A, os caracteres 'x' e 'y' apresentam correlação positiva, portanto uma seleção atuando somente sobre o caráter 'y' leva a um *aumento* correlacionado no caráter 'x'; de forma oposta, na situação B os caracteres 'x' e 'y' têm correlação negativa, e uma seleção atuando somente sobre o caráter 'y' leva a uma *redução* correlacionada no caráter x. Figura de Costa (2013).

Figura 1-2 - Tabelas de correlações entre três caracteres de duas espécies hipotéticas, A e B, e representações gráficas das correlações. As espécies neste caso mostram o mesmo *padrão* de integração (correlação negativa entre ZSZI e NSLZS e positiva entre as demais), mas *magnitudes* de integração distintas (maior em A que em B). Figura retirada de Porto *et al* (2009).

A possibilidade de utilizar matrizes de covariância fenotípicas (**P**) bem estimadas em estudos evolutivos como substitutas para matrizes genéticas (**G**), proposta inicialmente por Cheverud (1988), é hoje suportada por vários autores, em diferentes graus para diversos organismos e tipos de caracteres (Roff, 1995, 1996; Koots & Gibson, 1996; Simons & Roff, 1996; Tucic & Avramov, 1996; Bonnin *et al*, 1997; Reusch & Blanckenhorn, 1998; Waitt & Levin, 1998; Garcia *et al*, 2014). Esta substituição facilitou bastante a realização de estudos evolutivos da integração morfológica em populações naturais, já que estimativas de **G** dependem da disponibilidade de informações sobre relações genealógicas (Falconer & Mackay, 1996; Lynch & Walsh, 1998). Além disso, estimativas de matrizes **P** tendem a ser melhores que as de matrizes **G**, já que a estimação das últimas depende do número de *famílias* utilizadas, geralmente muito reduzido frente ao número amostral possível para estimativas de **P** (Roff, 1997). Os resultados de estudos comparando matrizes **P** e **G** para caracteres do crânio e mandíbula de mamíferos mostram alta similaridade entre as matrizes fenotípica e genética de uma mesma espécie em todos os casos (Cheverud, 1996; De Conto, 2007; Garcia *et al*, 2014).

Estudos de integração morfológica e modularidade podem ser realizados em níveis de organização distintos, refletindo diferentes aspectos da biologia dos organismos analisados (Klingenberg, 2014). Alguns trabalhos (ex. Monteiro & Nogueira, 2009; Goswami & Polly, 2010; Meloro & Slater, 2012) analisam a covariação entre populações (ou entre espécies), calculada a partir das diferenças entre médias dos caracteres por população (ou por espécie), refletindo a evolução coordenada de caracteres entre espécies, que pode ser causada tanto pela integração morfológica em nível intra-populacional quanto por pressões seletivas coordenadas entre caracteres (Felsenstein, 1988). Por outro lado, estudos focados na covariação intra-populacional ou intra-específica, considerando a exclusão de variações devidas a fatores externos como variações geografia e/ou dimorfismo sexual (e.g. Stepan, 1997a,b; Marroig & Cheverud, 2001, 2005; Goswami, 2006 a,b; Oliveira *et al*, 2009; Porto *et al*, 2009; Shirai & Marroig, 2010; Haber, 2015) procuram representar diretamente a integração morfológica no sentido definido por Olson & Miller (1958), refletindo aspectos genéticos, funcionais e ontogenéticos definidores das interações entre caracteres.

Estudos comparativos dos padrões e magnitudes de integração em diferentes clados são de grande interesse para análises sobre a evolução fenotípica, tanto pelas potenciais implicações evolutivas da covariação entre caracteres (Marroig *et al*, 2009)

como para compreender como a própria integração morfológica evolui em diferentes linhagens. Dada a importância do processo de desenvolvimento na estruturação da integração, processos de desenvolvimento comuns possivelmente levam a maior estabilidade na integração morfológica - algo efetivamente observado em estudos passados, principalmente com mamíferos (i.e. Steppan, 1997b; Marroig & Cheverud, 2001; Oliveira *et al*, 2009; Porto *et al*, 2009). Entretanto, variações entre clados estão presentes mesmo quando a integração é relativamente estável, podendo estar relacionadas a fatores históricos (i.e. filogenia) ou a pressões funcionais externas (p.ex aspectos ecológicos), que podem afetar tanto elementos da morfologia média quanto as associações entre diferentes caracteres. Assim, análises comparativas investigando as relações entre integração morfológica e história filogenética ou fatores ecológicos podem ajudar a compreender como, quanto e em quais condições a própria integração morfológica evolui.

Integração morfológica em Mamíferos

Resultados de diversos estudos sobre a integração morfológica no crânio em mamíferos em nível intra-específico e com ampla cobertura taxonômica, utilizando matrizes **P** (Marroig & Cheverud, 2001; Oliveira *et al*, 2009; Porto *et al*, 2009; Shirai & Marroig, 2010; Porto *et al*, 2013), revelaram alguns padrões que parecem gerais para mamíferos: I) a *magnitude* de integração mostra-se bastante variável, frequentemente com diferenças relevantes mesmo entre grupos filogeneticamente próximos; II) os *padrões* de integração parecem ser mais conservados na maior parte dos grupos (apesar de essa maior similaridade não necessariamente significar ausência de diferenças - Haber, 2015; ver também parágrafo abaixo); III) o principal fator relacionado a mudanças nas magnitudes de integração é a proporção de variação total composta por tamanho (medido como o primeiro componente principal da matriz de covariância, e portanto não separado entre tamanho isométrico e alométrico; Teissier, 1960; Jolicoeur, 1963); IV) maiores proporções de variação de tamanho produzem maiores correlações (i.e. maiores magnitudes de integração) e tendem a deixar os módulos menos evidentes, dificultando sua detecção (Porto *et al*, 2013). Estes resultados se baseiam em análises com ampla representação taxonômica em primatas neotropicais (Platyrrhini - Cheverud, 1996; Marroig & Cheverud, 2001; Shirai & Marroig, 2010), primatas antropóides do velho mundo (Catarrhini - Oliveira *et al*, 2009) e marsupiais (Didelphimorphia - Shirai & Marroig, 2010) e em análises de diversas famílias de mamíferos, representadas cada

uma por uma espécie ou gênero (Porto *et al*, 2009; Porto *et al*, 2013 - este último incluindo Felidae). Os resultados de teses de doutoramento recentes investigando clados adicionais parecem também corroborar estes padrões gerais (Xenarthra: Hubbe, 2013; roedores Sigmodontinae: Costa, 2013; morcegos filostomídeos: Rossoni, 2013).

A maior estabilidade dos padrões de integração em mamíferos em relação à magnitude de integração foi mencionada em uma série de trabalhos anteriores (e.g. Marroig & Cheverud, 2001; Porto *et al*, 2009; Oliveira *et al*, 2009), baseando-se nos valores de similaridade e em testes de significância para comparações de matrizes **P** entre clados. Os testes de significância realizados nestes estudos para matrizes de covariância utilizam o método de Adagas Aleatórias (*Random Skewers* - RS; descrito em Cheverud & Marroig, 2007), baseado na equação multivariada de resposta a seleção, para testar uma hipótese nula de "ausência de similaridade" entre matrizes, rejeitada em praticamente todos os casos. Marroig & Cheverud (2001) e Cheverud & Marroig (2007) também testam e rejeitam a hipótese nula de "ausência de diferenças" em diversos casos utilizando método distinto (Análise de Componentes Principais Comuns, CPCA - Airolidi & Flury, 1988); nestes casos, os autores consideram a rejeição da "ausência de similaridade" pelo método RS mais representativa, já que este método tem fundamentação na teoria evolutiva, enquanto que o método CPCA reconheceria diferenças significativas mesmo entre matrizes muito semelhantes. Recentemente, Haber (2015) utilizou o método RS para testar ambas as hipóteses ("ausência de diferenças" e "ausência de similaridade") em Ruminantes, mostrando que em diversos casos ambas são facilmente rejeitadas. Este resultado reforça uma ideia que já se encontrava presente nos estudos de Marroig & Cheverud (2001) e Cheverud & Marroig (2007): os padrões de integração de fato evoluem, e não são exatamente iguais em espécies distintas. Haber (2015) minimiza a relevância de testes de hipótese na comparação entre matrizes **P**, sugerindo focar as comparações não na significância, mas nos valores de similaridade e em como ocorre a evolução da integração morfológica: quais fatores influenciam sua evolução, e em quais escalas filogenéticas estas ocorrem (Roff, 2000; Steppan *et al*, 2002; Arnold *et al*, 2008).

Ressalta-se que, a despeito da discussão baseada na rejeição da hipótese de "ausência de similaridade" realizada em estudos anteriores (e.g. Marroig & Cheverud, 2001; Oliveira *et al*, 2009; Porto *et al*, 2009), esses próprios estudos iniciaram a investigação de várias das questões importantes sobre a evolução da integração mencionadas acima. Marroig & Cheverud (2001, 2005), por exemplo, mostraram que as

variações existentes na integração morfológica bastante conservada de primatas neotropicais não são correlacionadas à filogenia, mas são influenciadas em parte pela dieta. Porto *et al* (2009), trabalhando com representantes de diversos ordens de mamíferos, também não encontram relação entre padrões de integração e a filogenia, apesar de revelar uma aparente estruturação filogenética das magnitudes de integração (r^2). Oliveira *et al* (2009), por outro lado, encontram associações da integração tanto com a morfologia média quanto com a história filogenética nos primatas do velho mundo (Catarrhini), indicando a ocorrência de alterações na integração ao longo da filogenia do grupo - ainda que essas alterações sejam relativamente pequenas, já que os padrões de integração se mantêm notavelmente similares também em Catarrhini.

Ao menos outros dois estudos contribuíram para o conhecimento sobre a evolução da integração intra-populacional em mamíferos: Haber (2015), analisando a integração morfológica em Ruminantes (Artiodactyla), mostra alterações nos padrões de integração concentradas na base do grupo, na separação entre as famílias Bovidae e Cervidae, além de alguma variação dentro de cada família. Por fim, o trabalho de Goswami (2006a) com a ordem Carnivora mostra associações da integração morfológica com a filogenia em partes do grupo, incluindo Feliformia, e influências da dieta em certos grupos de Caniformia, mas não em Feliformia ou felídeos. Apesar destes primeiros estudos investigando a evolução da integração, nota-se ainda uma carência de estudos taxonomicamente inclusivos focados na estruturação e nos fatores relevantes para a evolução da integração em diversos clados. O próprio estudo de Goswami (2006a) tem representatividade taxonômica limitada, particularmente para a subordem Feliformia, e apresenta algumas particularidades metodológicas que podem afetar sua interpretação e comparabilidade com outros estudos de integração em mamíferos.

Feliformia

A sub-ordem Feliformia é um dos dois clados componentes da ordem Carnivora. O grupo tradicionalmente incluía quatro famílias recentes: Hyaenidae, Viverridae, Herpestidae e Felidae. Entretanto, os resultados de diversos trabalhos utilizando análises moleculares permitiram a resolução de uma série de incertezas taxonômicas, em especial dentro das famílias Viverridae e Herpestidae, levando alguns grupos de clados a serem elevados ao grau de famílias (e.g. Veron & Catzeflis, 1993; Flynn & Nedbal, 1998; Veron & Heard, 2000; Gaubert & Veron, 2003; Yoder *et al.*, 2003; Gaubert *et*

al., 2004a, 2004b) e resultando no arranjo atual, considerado relativamente consensual, que inclui sete famílias de espécies viventes (**Figura 1-3**): Felidae (gatos e panteras), Hyaenidae (hienas), Viverridae (civetas, ginetas, e “linsangs” africanos), Herpestidae (mangustos, cusimanses e suricates), Eupleridae (grupo endêmico de Madagascar, incluindo fossa, falanouc, civeta malgaxe e mangustos malgaxes), Prionodontidae (“linsangs” asiáticos) e Nandiniidae (incluindo uma única espécie, a "civeta de palmeira africana" *Nandinia binotata*). Entre estas sete famílias, e considerando espécies recentemente descritas, Feliformia reúne aproximadamente 130 espécies viventes, apresentando, portanto, riqueza similar à sub-ordem irmã (Caniformia). Este grupo apresenta diversidade marcante não só em termos de número de espécies, como também em variação de tamanho e ecomorfologia, sendo portanto um alvo particularmente interessante para análises comparativas da integração morfológica.

Figura 1.3 - Representantes das sete famílias atualmente incluídas na subordem Feliformia: *Panthera onca* (Felidae), *Crocuta crocuta* (Hyaenidae), *Suricata suricatta* (Herpestidae), *Civettictis civetta* (Viverridae), *Nandinia binotata* (Nandiniidae), *Galidia elegans* (Eupleridae) e *Prionodon pardicolor* (Prionodontidae).

Essa diversidade faz-se notar tanto entre as famílias do grupo como internamente a várias destas. **Felidae**, inteiramente composta por animais hipercarnívoros (Van Valkenburgh, 1988), tem entre seus representantes recentes grande variação de tamanho, mas variação de forma menor, com um padrão craniano geral *cat-like* (Martin, 1989), explicada principalmente por relações alométricas dentre as espécies da família (Werdelin, 1983; Slater & Van Valkenburgh, 2009; Christiansen,

2008a; Sicuro, 2011; Sakamoto & Ruta, 2012; Meloro & Slater, 2012), apesar de algumas variações não relacionadas ao tamanho serem reconhecidas (Christiansen, 2008b; Sicuro, 2011; Sakamoto & Ruta, 2012). Os felídeos apresentam também algumas variações no grau de socialidade de seus representantes: enquanto a maior parte das espécies é solitária e não apresenta comportamentos cooperativos, algumas espécies apresentam comportamento de caça coordenada entre dois ou mais indivíduos (diversos *Lynx* - Bailey *et al*, 2013) e em alguns casos também outros padrões sociais (*Acinonyx jubatus*, *Panthera uncia* e *P. leo* - Smith *et al*, 2012; *Felis catus* - Macdonald *et al*, 2000). **Hyaenidae**, com apenas quatro representantes vivos, inclui uma espécie (*Crocuta crocuta*) que consome presas maiores e possui especialização para permitir quebra dos ossos ('*bone-cracking*') de suas presas, duas espécies também com adaptações para o consumo de ossos (Werdelin & Solounias 1991; Joeckel, 1998; Ferretti, 2007) mas consideradas mais generalistas, e uma espécie mirmecófaga (aardwolf, *Proteles cristata*), parte desta variação refletindo-se na morfologia craniana (Tseng & Wang, 2011). As hienas viventes apresentam também interessante gradação em seu grau de socialidade (Holekamp *et al*, 2015) variando desde o aardwolf, solitário (Richardson, 1988) até a hiena malhada, *Crocuta crocuta*, que vive em grandes clãs e apresenta complexidade social comparável à de diversos primatas (Holekamp *et al*, 2012). **Herpestidae** (mangustos) inclui principalmente animais que se alimentam primariamente de invertebrados, ou de invertebrados e pequenos vertebrados, e abrange tanto espécies solitárias quanto outras altamente sociais, a maior parte das últimas agrupadas em um grupo monofilético (Veron *et al*, 2004). **Eupleridae** (carnívoros malgaxes), grupo proposto como monofilético por Yoder *et al* (2003) e corroborado em análises posteriores, abarca notável variação morfológica, mostrando marcantes convergências com outros grupos, como a de *Cryptoprocta ferox* com felinos (van Valkenburgh, 2007), a de *Galidia*, *Galidictis*, *Salanoia* e *Mungotictis* com herpestídeos (*mongoose-like*, Yoder *et al*, 2003), e a de *Fossa* e *Eupleres* com viverrídeos *sensu strictu* (Gaubert *et al*, 2005a). Os carnívoros de Madagascar apresentam também grande variação ecológica, incluindo representantes primariamente carnívoros (*Cryptoprocta*, *Galidictis*), insetívoros, onívoros, e um gênero (*Eupleres*) que se alimenta preferencialmente de larvas e minhocas (Albignac, 1974), bem como alguma variação de socialidade (Smith *et al*, 2012). **Viverridae** em seu sentido atual inclui somente espécies solitárias, mas tem considerável variação morfológica e de dieta, incluindo onívoros (p.ex. *Civettictis civetta*), insetívoros (p.ex. *Hemigalus derbyanus*) e animais

principalmente frugívoros (p.ex. *Paradoxurus*). Entre as famílias menos inclusivas, anteriormente incluídas entre os viverrídeos, **Nandiniidae** conta com apenas uma espécie (*Nandinia binotata*) morfológicamente similar a outros viverrídeos, solitária e onívora, com preferência por frutos (Charles-Dominique, 1978); **Prionodontidae**, atualmente considerada pela maior parte dos estudos como grupo irmão de Felidae (Gaubert & Veron, 2003; Barycka, 2007; Eizirik *et al*, 2010; Nyakatura & Bininda-Emonds, 2012), tem dois representantes asiáticos solitários (gênero *Prionodon*), morfológicamente similares ao gênero viverrídeo africano *Poiana* quanto à dentição, pelagem, ultra-estrutura dos pelos, proporções corpóreas e também à forma do crânio (Gaubert & Veron, 2003; Gaubert *et al*, 2005a). É interessante que, embora *Prionodon* e *Poiana* compartilhem uma dentição considerada hipercarnívora (Wozencraft, 1984) e habitats similares (Gregory & Hellman, 1939; Crawford-Cabral, 1981; 1993), *Poiana* seja basicamente onívoro (Nowak, 1999), enquanto a evidência limitada sobre a dieta dos *linsangs* asiáticos sugere que estes sejam primariamente carnívoros (Davis, 1958; Lim, 1973; Phang-Chong-Ahn, 1980). Verifica-se, assim, que a frequência e grau de convergências morfológicas em Feliformia é também notável, fornecendo mais um motivo de interesse para estudos comparativos de integração morfológica e restrições evolutivas no grupo, juntamente à variação existente nos graus de socialidade e dieta (para a última, particularmente fora de Felidae, de longe a família mais estudada do grupo).

As relações filogenéticas em Feliformia são ainda foco de discussões, apesar de o reconhecimento das sete famílias mencionadas acima ser considerado atualmente consensual, como mostram a revisão da sistemática e evolução do grupo publicada por Barycka (2007) e trabalhos recentes como os de Eizirik *et al* (2010) e Agnarsson *et al* (2010) e a super-árvore de Nyakatura & Bininda-Emonds (2012). As divergências anteriores quanto às relações de parentesco entre as famílias mostram-se também basicamente já resolvidas, sendo consensuais a posição basal de Nandiniidae como grupo irmão dos demais Feliformia (como sugerido por Flynn & Nedbal, 1998; Wesley-Hunt & Flynn, 2005; Flynn *et al*, 2005) e a posição de Eupleridae como grupo irmão de Herpestidae, inicialmente postulada por Yoder *et al*. (2003). A alocação de Prionodontidae, posicionada por Gaubert & Veron (2003) como grupo irmão de Felidae, é contestada por Agnarsson *et al* (2010), que coloca os *linsangs* asiáticos como grupo irmão de Hyaenidae + (Eupleridae; Herpestidae), mas atualmente a maior parte dos trabalhos corrobora seu alinhamento aos felídeos (Barycka, 2007; Eizirik *et al*, 2010;

Nyakatura & Bininda-Emonds, 2012), respaldando assim um arranjo taxonômico relativamente bem-resolvido.

As relações filogenéticas dentro de cada família do grupo, por outro lado, são ainda discutidas, e novas espécies continuam a ser descritas. Alguns trabalhos recentes têm contribuído para um cenário mais claro quanto à sistemática e taxonomia de cada família. Incluem-se aí, para Felidae, trabalhos como os de Johnson *et al* (2006) e Li *et al*, 2016, que propõem uma topologia praticamente consensual para o grupo e resolvem inconsistências decorrentes de hibridização entre linhagens; o de Driscoll *et al* (2007), que dá uma resposta mais clara quanto à origem dos gatos domésticos (*Felis catus*) e sua relação com gatos selvagens (*F. silvestris*); o de Trigo *et al*, 2013, que propõe a divisão de *Leopardus tigrinus* em *L. tigrinus* e *L. guttulus*; o artigo de Wilting *et al* (2007), que propõe a divisão de *Neofelis* em *N. nebulosa* e *N. diardi*; a revisão taxonômica de *Leopardus* de Nascimento (2010); e uma série de trabalhos lidando com a filogeografia de diferentes espécies (p.ex. Janečka *et al*, 2007). Para Hyaenidae, o trabalho de Koepfli *et al* (2006) apresenta uma topologia respaldada por trabalhos mais inclusivos abarcando as hienas, considerada agora praticamente consensual para a família. Em Viverridae são importantes os diversos trabalhos de Phillipe Gaubert e colaboradores, que clarearam um pouco as relações entre as diversas espécies de *Genetta* (Gaubert *et al*, 2004a, b; Gaubert *et al*, 2005b), bem como outros trabalhos do grupo de Géraldine Veron (Veron & Heard, 2000; Patou *et al*, 2008, 2010; Veron *et al*, 2014; Veron *et al*, 2015a) e o de Wilting & Fickel (2012) que lidam com outros grupos de espécie na família e propõem a separação de *Arctogalidia trivirgata* em duas espécies (*A. trivirgata* e *A. stigmatica*). Dentro de Herpestidae, a resolução das relações filogenéticas também deve muito ao grupo de Géraldine Veron, que mostrou a monofilia de um grupo incluindo a maior parte dos mangustos sociais (Veron *et al*, 2004) e dos "*Herpestes*" asiáticos (Patou *et al*, 2009; Veron *et al*, 2015b), ao mesmo tempo mostrando a polifilia do gênero *Herpestes* tradicionalmente reconhecido e propondo o uso de *Urva* para as espécies asiáticas e *Xenogale naso* para o mangusto-de-nariz-longo, apontado como grupo irmão de *Atilax paludinosus*. São também relevantes para Herpestidae: o trabalho de Rapson *et al* (2012), que analisa o grupo até então pouco estudado dos pequenos mangustos solitários africanos (gênero *Galerella*), sugerindo a parafilia de uma espécie tradicionalmente reconhecida (*Galerella sanguinea*), que possivelmente representa duas espécies distintas; o de Perez *et al* (2006), que lida com as relações sistemáticas no gênero *Bdeogale*; e o de Sonet *et al*

(2014), que estuda relações filogenéticas e craniometria no gênero *Crossarchus*. Em Eupleridae, as relações entre espécies foram estudadas basicamente apenas por Yoder *et al* (2003) e alguns trabalhos com cobertura taxonômica mais ampla, geralmente não incluindo todas as espécies do grupo (p.ex. Agnarsson *et al*, 2010). Há, entretanto, trabalhos recentes descrevendo novas espécies de carnívoros malgaxes com base em caracteres morfológicos (Wozencraft, 1986 - *Galidictis grandidieri*; Durbin *et al*, 2010 - *Salanoia durrelli*) e propondo a separação de uma espécie tradicional (*Eupleres goudotii*) baseada em divergências genéticas (Goodman & Helgen, 2010). Como vários destes estudos detalhados dentro de cada família são posteriores ao período de coleta de dados para a filogenia completa mais inclusiva de Carnivora (Nyakatura & Bininda-Emonds, 2012), grande parte dos resultados mais recentes não se encontram refletidos nela. Por esta razão, decidiu-se no presente trabalho utilizar como base para as análises em contexto filogenético uma filogenia baseada na de Nyakatura & Bininda-Emonds (2012) com algumas alterações refletindo resultados de outros estudos recentes, como se descreve no **Capítulo II** e no **Anexo 10** (em inglês).

Evolução morfológica e integração em Feliformia

As relações entre tamanho, dieta e forma e sua relevância para a evolução das espécies de Feliformia foram investigadas em diversos estudos (p.ex. Mattern & McLennan, 2000; Christiansen & Wroe, 2007; Wroe & Milne, 2007; Slater & van Valkenburgh, 2008, 2009; Meachen-Samuels & van Valkenburgh, 2009; Sicuro, 2011; Sicuro & Oliveira, 2011; Tseng & Wang, 2011; Sakamoto & Ruta, 2012; entre outros). Há também vários trabalhos que analisam restrições evolutivas no crânio em Carnivora (p.ex. Holiday & Stepan, 2004; Meiri *et al*, 2005; Goswami, 2006a, b; Christiansen, 2008b; Goswami & Polly, 2010; Goswami *et al*, 2011; Figueirido *et al*, 2010; Meloro & Slater, 2012; Cardini & Polly, 2013), além de um trabalho recente tratando sobre a integração morfológica no pós-crânio de carnívoros (Martín-Serra *et al*, 2015). Ressalta-se, entretanto, que a subordem Feliformia é representada em grande parte destes trabalhos somente por Felidae e/ou Hyaenidae, ou em alguns casos por poucos representantes das demais famílias; o trabalho de Christiansen & Wroe (2007) sobre forças de mordida é uma das poucas exceções, incluindo diversas espécies de viverrídeos e herpestídeos. Além disso, a grande maioria destes trabalhos baseia-se principalmente em padrões de agrupamento de formas para realizar inferências sobre restrições evolutivas, não tratando direta e explicitamente os padrões e/ou magnitudes

de integração morfológica e sua estruturação filogenética ou sua relação com aspectos da ecologia das espécies. Podem-se mencionar como exceções os trabalhos de Goswami (2006a) e Goswami & Polly (2010).

Goswami & Polly (2010) propõem-se a avaliar a influência da integração sobre a diversificação morfológica em Carnivora e primatas. Os autores interpretam seus resultados como indicativos de que, quando existente, o efeito de uma forte integração entre caracteres seria a limitação da variação morfológica. Entretanto, o trabalho baseia-se em comparações entre as médias dos caracteres para diferentes espécies, analisando portanto padrões de covariação inter-específicos. Uma vez que a covariação inter-específica pode resultar tanto da integração morfológica intraespecífica quanto de seleção correlacionada entre caracteres (Felsenstein, 1988; Zeng, 1988), o estudo de Goswami & Polly (2010), como outros focados na integração inter-específica, tem limitações a suas possíveis interpretações evolutivas.

O trabalho de Goswami (2006a), já mencionado acima, busca relacionar a integração morfológica intra-específica com a filogenia e a dieta para diferentes grupos dentro de Carnivora. A autora encontra associações da integração morfológica com a história filogenética para Carnivora como um todo e diversos de seus subgrupos: Caniformia, Canidae, Musteloidea, Mustelidae, bem como Feliformia e Felidae. Além disso, encontra influências da dieta sobre a integração em Caniformia, Arctoidea (Ursidae + Procyonidae + Mustelidae), Musteloidea (Procyonidae + Mustelidae) e Mustelidae, mas não dentro de Feliformia ou Felidae.

Os dois trabalhos existentes que procuraram avaliar de forma mais explícita a integração morfológica e suas implicações evolutivas em Feliformia lidam com amostras relativamente reduzidas: Goswami (2006a) analisa 12 representantes de Feliformia: 5 espécies de Felidae (incluindo *Smilodon fatalis*, extinta), 2 de Herpestidae, 2 de Viverridae, 2 de Hyaenidae e 1 de Eupleridae (*Galidia elegans*, incluída no trabalho ainda em Herpestidae), com amostras variando entre 15 e 21 espécimes por espécie; Goswami & Polly (2010) utilizam 4 espécies de Felidae, 4 de Herpestidae, 4 de Eupleridae, 3 de Viverridae, 2 de Hyaenidae e *Nandinia binotata*, a maior parte das espécies representada por somente dois exemplares (um macho e uma fêmea), já que o trabalho mede a integração intra-específica. No estudo de Goswami (2006a), o uso de amostras relativamente reduzidas em relação ao número de caracteres para quase todas

as espécies pode, ainda, resultar em imprecisões na estimação da variabilidade intra-populacional.

Soma-se a isso que os trabalhos de Goswami (2006a) e Goswami & Polly (2010) utilizam métodos de morfometria geométrica, diferentemente de outros estudos de integração morfológica com ampla cobertura taxonômica e centrados em medidas diretas da variação disponível para os processos evolutivos (como Marroig & Cheverud (2001, 2005), Marroig *et al* (2009) e Porto *et al* (2009), que utilizam análises de distâncias lineares. Esta diferença dificulta a comparação entre os resultados dos estudos existentes, e há indicações de que o uso de variáveis resultantes de análises de Procrustes (como é o caso com métodos de morfometria geométrica) na estimativa de padrões de covariação pode ser problemático e causar distorções da estrutura de covariação em alguns casos, como mencionado por Adams (2004) e van der Linde & Houle (2009).

Uma questão adicional é que estudos de covariação baseados em morfometria geométrica necessitam decidir entre incluir grande número de variáveis (tratando as coordenadas x, y e z de cada marco anatômico como uma variável distinta) ou utilizar métodos para obter "correlações únicas" entre pares de marcos anatômicos multidimensionais (p.ex. correlações canônicas; Hotelling, 1936; ou coeficientes de congruência; Burt, 1948, Tucker, 1951), que poderiam alterar a estrutura do espaço representado em alguns casos. Adams (2015) identificou também recentemente que o índice RV, frequentemente utilizado em estudos de morfometria geométrica como medida de integração (e semelhante ao coeficiente de congruência; Abdi, 2007), apresenta vieses relacionados ao número amostral e ao número de caracteres. Similarmente, Garcia *et al* (*in prep*) encontraram que o uso de resíduos de Procrustes para a identificação de padrões modulares resulta em baixo poder em comparação ao uso de distâncias lineares, e que o mesmo ocorre com o uso do índice RV para este propósito independente das variáveis utilizadas. É provável, portanto, que o uso de técnicas de morfometria geométrica para análises de integração morfológica e modularidade resulte em dificuldades na interpretação dos resultados e/ou na comparabilidade entre estudos.

Objetivos

Esta dissertação segue direção semelhante a trabalhos anteriores que analisaram padrões e magnitudes de integração em mamíferos, como os de Goswami (2006a), Marroig & Cheverud (2001, 2005), Marroig *et al* (2003, 2009), Porto *et al* (2009), Oliveira *et al* (2009) e Shirai & Marroig (2010) e as teses de Hubbe (2013), Costa (2013) e Rossoni (2013). O trabalho propõe-se a analisar padrões e magnitudes de integração em Feliformia, com ampla representatividade taxonômica e números amostrais altos sempre que possível. Propõe também comparar os padrões e magnitudes de integração com a morfologia média, história filogenética do grupo e fatores ecológicos (dieta e socialidade), buscando assim compreender como ocorre a evolução da integração morfológica no grupo e identificar possíveis fatores que influenciam essa evolução. Utilizam-se aqui técnicas de morfometria baseadas em distâncias lineares, permitindo comparação direta com resultados de estudos de integração em mamíferos já publicados e/ou atualmente em elaboração. Esta dissertação representa, assim, uma contribuição relevante para o estudo do grupo, além de abrir possibilidades para estudos futuros sobre a organização modular do crânio, as implicações evolutivas da integração morfológica em Feliformia e outros temas relacionados. Análises da estruturação modular do crânio em Feliformia foram parcialmente realizadas durante a preparação desta dissertação, mas não são apresentadas aqui. Análises adicionais e mais detalhadas sobre a modularidade do crânio em Feliformia encontram-se atualmente em preparação, e serão objeto de artigos posteriores.

Os objetivos específicos primários e secundários incluídos nesta dissertação foram:

I) Caracterização do padrão e da magnitude de integração fenotípica nas diferentes espécies e famílias de Feliformia. Este objetivo pode ser subdividido em algumas partes:

I.a) Comparação do padrão de integração fenotípica por meio de comparações das matrizes de covariância de diversas espécies/grupos;

I.b) Comparação da magnitude de integração fenotípica utilizando índices de integração, e de potenciais consequências evolutivas das diferenças na integração, refletidas em métricas relacionadas às matrizes de covariância;

I.c) Identificação da quantidade de variação isométrica em cada grupo, testando a hipótese de que Felidae tem variação *intraespecífica* principalmente

relacionada ao tamanho, como encontrado em outros estudos para a variação entre grupos e analisando a relação entre variação isométrica e integração;

I.d) Identificação dos caracteres cujo padrão de respostas à seleção difere mais frequentemente entre as espécies e daqueles cujo padrão de respostas é mais similar ao padrão *geral* de respostas à seleção;

II) Investigação de possíveis fatores influenciando o padrão e a magnitude de integração em Feliformia. Este objetivo incluiu análises da influência das relações filogenéticas entre os grupos, dois fatores ecológicos (dieta e socialidade), bem como a inter-relação entre morfologia média, tamanho corpóreo, padrões e magnitudes de integração. As análises relacionadas a este objetivo ocorreram de duas formas distintas:

Ila) Fatores relacionados a padrão e magnitude de integração considerando as matrizes de covariância completas;

Ilb) Fatores relacionados ao padrão de respostas à seleção de caracteres particulares;

III) Comparação de padrões e magnitudes encontrados para Feliformia com os resultados encontrados para outros grupos de mamíferos.

Estrutura da Dissertação

A forma escolhida para tratar estes objetivos integrou as análises em um único capítulo. Este trata os três objetivos primários com base nos padrões de integração no crânio de forma geral, sem foco nos padrões modulares reconhecíveis, e centra-se em análises das magnitudes e padrões de integração, nos fatores relacionados a estes e na contextualização destes aspectos em Feliformia com relação a outros mamíferos. Dado o grande volume de resultados, planeja-se subdividi-los em artigos focados em temas mais específicos para posterior publicação em periódicos.

Hipóteses

Com base na fundamentação teórica sobre os fatores que influenciam a integração morfológica e nos resultados de estudos prévios sobre a evolução da integração fenotípica em carnívoros e mamíferos como um todo, podem-se levantar hipóteses *a priori* (i.e. expectativas prévias) a respeito de alguns dos aspectos

envolvidos nos objetivos primários deste trabalho. Estas hipóteses são explicitadas abaixo. Alguns dos aspectos analisados não contam com resultados prévios ou fundamentação suficiente para sustentar hipóteses *a priori*. Nestes casos, indica-se abaixo que o presente trabalho os analisa de forma exploratória.

Objetivos 1 e 3 - Aspecto 1 - Padrões de Integração.

Hipótese: Padrões de integração similares entre clados

A integração morfológica intra-populacional é diretamente afetada pelos processos de desenvolvimento (Cheverud, 1982, 1984), que mostram-se bastante conservados em mamíferos (Moore, 1981; Smith, 1997; Tapadia *et al*, 2005). Dessa forma, seria razoável esperar que os padrões de integração morfológica em mamíferos sejam relativamente estáveis. De fato, altas similaridades nos padrões de integração foram encontradas por Porto *et al* (2009) entre representantes de diferentes ordens de mamíferos, bem como por Marroig & Cheverud (2001) e Oliveira *et al* (2009) em primatas, sustentando a ideia de que um padrão de integração conservado seja mantido em mamíferos por seleção estabilizadora interna, com preservação do desenvolvimento e das funções gerais do crânio de mamíferos (Cheverud, 1996b; Marroig & Cheverud, 2001; Porto *et al*, 2009). Teses de doutoramento recentes lidando com outros grupos de mamíferos (Hubbe, 2013; Costa, 2013; Rossoni, 2013) encontraram também similaridades altas entre outros grupos de mamíferos, dando mais suporte a essa hipótese.

Os resultados obtidos por Goswami (2006a) para Feliformia também parecem mostrar similaridade tão ou mais alta entre os representantes incluídos dessa subordem que aquela vista entre representantes de outros grupos de mamíferos.

Objetivos 1 e 3 - Aspecto 2 - Magnitudes de integração.

Hipótese: Magnitude de integração mais variável entre clados que os padrões de integração

Apesar de a existência de um processo de desenvolvimento preservado entre os mamíferos aparentemente levar à manutenção de padrões de integração similares, isso não significa que a integração se mantenha exatamente igual entre diferentes táxons. Em particular, enquanto os processos de desenvolvimento similares parecem levar a uma preservação de quais conjuntos de caracteres apresentam maiores covariações, a intensidade geral das correlações entre caracteres do crânio (i.e. a magnitude de integração) aparentemente pode se manter bastante variável mesmo entre clados

filogeneticamente próximos, como mostram a comparação entre diferentes ordens de mamíferos de Porto *et al* (2009) e também os trabalhos de Oliveira *et al* (2009), Hubbe (2013), Costa (2013) e Rossoni (2013). Como mostrado por Marroig *et al* (2009) e Porto *et al* (2013), a magnitude de integração em mamíferos é fortemente correlacionada à quantidade de variação reunida no primeiro componente principal das matrizes de covariância fenotípica, que pode ser compreendido como uma medida da variação de tamanho em um táxon. De fato, o crescimento somático é apontado por Hallgrímsson *et al* (2007) como último de uma série de processos importantes para a estruturação da integração morfológica, produzindo covariação entre diferentes partes do crânio (geralmente de forma mais acentuada na face). Como apontado por Porto *et al* (2013), é possível que a variação na magnitude de integração encontrada entre mamíferos reflita diferenças na intensidade e tempo de duração do próprio processo de crescimento somático no contexto do desenvolvimento de diferentes espécies. Dessa forma, diferenças na magnitude de integração poderiam se originar de diferenças nas particularidades de uma parte específica de um processo de desenvolvimento basicamente compartilhado entre os mamíferos, permitindo maior variação mesmo entre grupos filogeneticamente próximos.

Informações prévias sobre a magnitude de integração em carnívoros especificamente limitam-se aos valores reportados em Porto *et al* (2009), Porto (2009) e Porto *et al* (2013). *Cerdocyon*, *Leopardus* e *Nasua* apresentam magnitudes de integração relativamente altos ($r^2 \sim 0.21$), enquanto *Eira* tem valor mais baixo ($r^2 \sim 0.13$) e *Conepatus* é mais integrado ($r^2 \sim 0.34$). Baseando-se nesses valores, esperaria-se magnitude de integração média relativamente alta, mas potencialmente bastante variável em Carnivora. Lembra-se, entretanto, que somente um dos clados previamente analisados é representante da subordem Feliformia, analisada aqui.

Objetivo 1 - Aspecto 3 - Proporção de variação isométrica

Hipótese: Maior proporção de variação isométrica em Felidae em relação a outras famílias

Esta hipótese parte de diversas análises da morfologia craniana nos felídeos, que usualmente caracterizam a família como possuindo pouca variação de forma entre espécies, geralmente considerada principalmente alométrica, em contraste com grande variação de tamanho (Werdelin, 1983; Christiansen, 2008a; Slater & Van Valkenburgh,

2009; Sicuro, 2011; Sakamoto & Ruta, 2012; Meloro & Slater, 2012). Nenhum destes trabalhos comparou explicitamente a proporção de variação isométrica intra-específica entre felídeos e outros grupos, representando portanto um aspecto da variação inter-específica. Essa grande dominância da variação de tamanho entre espécies de felídeos poderia se originar de seleção ocorrendo exatamente na direção de tamanho, de restrições na própria variação intra-populacional nas diferentes espécies do grupo ou ainda de ambos estes fatores. O presente trabalho não analisa a variação inter-específica e não testa as possíveis formas de seleção envolvidas na diversificação dos diferentes grupos. Supõe-se aqui, entretanto, que a alta variação isométrica existente entre espécies provavelmente reflete, ao menos em algum grau, uma situação similar na variação intra-específica de Felidae.

Objetivo 1 - Aspecto 4 - Padrões de resposta a seleção caráter-específicos

Sem hipótese *a priori*

A caracterização de padrões de resposta a seleção caráter-específicos (SRD - Marroig *et al*, 2011) é uma adição relativamente nova ao conjunto de ferramentas da genética quantitativa para análises comparativas de integração morfológica, e sua utilização até o momento foi restrita a poucas teses de doutoramento ainda não publicadas em formato de artigo (Hubbe, 2013; Costa, 2013; Rossoni, 2013). Alguns caracteres correspondentes àqueles utilizados aqui mostraram padrões de resposta a seleção distintivos nestes três trabalhos (ZS-ZI, APET-TS, BA-OPI). Entretanto, não parece haver informações suficientes ou uma boa razão teórica para formular uma hipótese *a priori* bem fundamentada sobre este aspecto. Desta forma, essa análise é realizada de forma exploratória no presente trabalho.

Objetivo 2 - Aspectos 1 e 2 - Fatores relacionados a padrões e magnitudes de integração.

a) Padrão x magnitude

Sem hipótese *a priori*: Padrões e magnitudes de integração fenotípica são duas facetas de um fenômeno único: a estruturação da covariação entre diferentes caracteres, produzida ao longo da ontogenia por uma série de diferentes processos geradores de covariação (Hallgrímsson *et al*, 2007, 2009). Como mencionado acima, a magnitude de integração aparentemente está relacionada principalmente ao crescimento somático, último desses processos geradores de covariação a ocorrer ao longo da ontogenia. Já que

os diversos outros processos geradores de integração provavelmente têm maior efeito sobre os padrões de integração, mas pouco sobre as magnitudes, uma correlação de padrões e magnitudes entre espécies não necessariamente é esperada. Entretanto, maiores efeitos do processo de crescimento somático durante o desenvolvimento poderiam levar a um aumento da correlação e, ao mesmo tempo, a uma maior similaridade nos padrões de integração (já que estes possivelmente refletirão em maior grau a covariação imposta por este processo que a resultante de processos anteriores). Dessa forma, não parece haver fundamentação teórica para uma hipótese *a priori* clara quanto à correlação entre padrões e magnitudes de integração. A correlação entre padrões e magnitudes foi testada por Porto et al (2009) e Oliveira et al (2009), e também nas teses de doutoramento de Hubbe (2013), Costa (2013) e Rossoni (2013), encontrando resultados distintos nos diferentes estudos. Para Carnívora, não há até o momento nenhuma análise da relação entre padrões e magnitudes. O presente trabalho, portanto, realiza esta análise de forma exploratória.

b) Filogenia

Hipótese: Padrões de integração tendem a apresentar sinal filogenético em Feliformia.

Ainda que os padrões de integração em mamíferos sejam geralmente semelhantes, possivelmente como resultado de um processo de desenvolvimento compartilhado, variações na integração entre táxons existem, e podem se estruturar de diferentes formas. O fator possivelmente mais óbvio que pode influenciar a estruturação da integração é a história filogenética dos grupos, com padrões de integração mostrando-se mais similares entre táxons filogeneticamente próximos, e mais distintos entre táxons distantes. Um sinal filogenético sobre os padrões de integração pode ser esperado porque táxons mais distantes tiveram maior tempo para acumular divergências, inclusive em sua covariação fenotípica. Ao mesmo tempo, espécies que compartilham grande parte de sua história evolutiva possivelmente estiveram sujeitas a pressões adaptativas comuns que podem também ter afetado seus padrões de integração.

Apesar dessa relação ser uma hipótese nula óbvia, ela nem sempre foi encontrada em trabalhos prévios com mamíferos: uma estruturação dos padrões de integração segundo a filogenia foi encontrada por Oliveira *et al* (2009) para os primatas do velho mundo e também por Haber (2015) em Ruminantes (com diferenciação principalmente no nível das famílias), mas não por Marroig & Cheverud (2001) para primatas do novo mundo e Porto et al (2009) para representantes de diferentes ordens de

mamíferos. O estudo anterior com Carnívoros de Goswami (2006a) encontrou correlação entre padrões de integração e distâncias filogenéticas incluindo tamanhos de ramo em Feliformia, e encontra também uma relação com a filogenia em Felidae quando utilizando distâncias filogenéticas patrísticas (i.e. com tamanhos de ramo iguais). A análise da autora para Felidae inclui somente 5 espécies, e nenhuma outra família de Feliformia contava com número de espécies suficiente para testar a relação entre integração e filogenia. Ainda assim, pelas razões explicitadas acima, a existência de relação entre padrões de integração e filogenia é considerada aqui como uma hipótese nula válida para Feliformia como um todo e para agrupamentos filogenéticos menos inclusivos.

Sem hipótese *a priori*: Como mencionado acima, a magnitude de integração mostra uma forte associação com a proporção de variação no tamanho e, portanto, possivelmente também à intensidade do processo de crescimento somático. Considerando isso, a magnitude de integração tenderia a relacionar-se à filogenia se o próprio crescimento somático seguir uma estruturação filogenética. Porto *et al* (2009) mostram que a magnitude de integração se estrutura filogeneticamente entre representantes de diferentes ordens de mamíferos. O gráfico presente em Porto *et al* (2013) parece indicar também que uma medida da energia metabólica dedicada ao crescimento pós-natal (Eg - West *et al*, 2011) segue uma estruturação entre grupos filogenéticos mais inclusivos, com valores geralmente mais baixos entre morcegos, intermediários em diversos outros Eutheria e mais altos em Metatheria. Apesar disso, não há dados claros mostrando uma estruturação filogenética do crescimento somático ou da própria magnitude de integração como uma regra válida internamente para grupos filogenéticos menos inclusivos. Trabalhos anteriores que analisaram a relação entre magnitude de integração e filogenia tiveram resultados contraditórios: Oliveira *et al* (2009 - primatas do velho mundo), Costa (2013 - roedores Sigmodontinae) e Rossoni (2013 - morcegos filostomídeos) não encontraram estruturação filogenética nas magnitudes de integração, enquanto Hubbe (2013 - Xenarthra) encontrou este tipo de relação. Considera-se aqui, então, que não há fundamentação teórica ou resultados prévios suficientes para adotar uma hipótese *a priori* quanto à existência de associação entre filogenia e magnitudes de integração. Por esta razão, esta associação é testada aqui de forma exploratória.

c) Morfologia

Sem Hipótese a priori: As covariâncias genéticas entre caracteres (e portanto a integração morfológica) evoluem de forma a corresponder a efeitos mutacionais e ao padrão geral de seleção estabilizadora (Lande, 1980; Cheverud, 1996b). A seleção estabilizadora, por sua vez, é afetada por seleção externa (i.e. devido a fatores ambientais) e interna (resultante de interações entre os caracteres e características internas do próprio organismo). Segundo o modelo de Lande (1980), em situações nas quais os padrões de seleção estabilizadora e efeitos mutacionais se mantêm constantes os padrões de integração morfológica permanecem estáveis, mas as médias dos caracteres podem evoluir por deriva ou em resposta à seleção externa. Um desacoplamento da evolução da morfologia média e da integração, condizente com este modelo, foi encontrada nos primatas neotropicais (Marroig & Cheverud, 2001), e também em *Xenarthra* (2013). Em algumas situações, entretanto, a evolução da morfologia média pode levar a mudanças associadas também nos padrões de integração, como foi encontrado por Oliveira *et al* (2009), Costa (2013) e Rossoni (2013), ou também nas magnitudes de integração, como encontrado em Costa (2013).

De acordo com a fundamentação teórica existente, a evolução de padrões e magnitudes de integração morfológica pode ou não mostrar-se correlacionada à evolução da morfologia média, dependendo dos padrões de seleção aos quais um determinado grupo esteve sujeito. Considerando esse fato e a ausência de outros dados que sugiram uma hipótese prévia mais provável, a investigação de associações entre a evolução da morfologia média e da integração morfológica é realizada aqui de forma exploratória.

d) Tamanho

Sem hipótese a priori: Apesar de a variação de tamanho ser um fator fortemente relacionado à magnitude de integração (Porto *et al*, 2013), a única análise já realizada que testa a relação do tamanho médio dos crânios com aspectos relacionados à integração é a de Marroig *et al* (2009), onde não se encontra relação entre o tamanho do crânio e a magnitude de integração. Uma associação entre tamanho e padrões ou magnitude de integração teoricamente poderia ser esperada caso o maior tamanho esteja associado com maior integração em determinadas partes do crânio para manutenção da funcionalidade. Não há, entretanto, justificção teórica suficiente para considerar uma

hipótese *a priori* sobre este tipo de associação. Dessa forma, análises relacionando o tamanho médio à integração morfológica são realizadas aqui com caráter exploratório.

e) Dieta

Hipótese: Variações na dieta tendem a estar relacionadas a diferenças nos padrões de integração, principalmente em regiões mais diretamente relacionadas à obtenção de alimento e mastigação (regiões oral e zigomática).

Dado que a obtenção de alimento e a mastigação são duas das principais funções desempenhadas pelas estruturas presentes na cabeça de mamíferos, a dieta é um dos principais fatores externos que pode afetar a evolução craniana. Este fator pode afetar não somente os valores médios dos caracteres do crânio, mas também a estrutura de covariação entre caracteres, seja indiretamente por meio de seleção direcional para alterações nas médias gerando alterações correlacionadas na covariação, seja diretamente por meio de seleção sobre os próprios padrões de integração funcional (Marroig & Cheverud, 2001). Se a dieta efetivamente exercer uma influência sobre os padrões de integração, é provável que seus efeitos sejam particularmente fortes sobre as partes do crânio que se relacionam mais diretamente às funções de mastigação e obtenção de alimento. Assim, efeitos da dieta são esperados particularmente nas subregiões oral (relacionada ao desenvolvimento e suporte dos dentes e ao crescimento da língua e epitélio oral - Ferguson, 1988; Cheverud, 1995) e zigomática (onde se encontra a origem da musculatura mastigatória massetérica - Cheverud, 1995).

O estudo de Goswami (2006a) não identificou efeitos da dieta sobre a integração em Feliformia (Goswami, 2006a), mas uma observação dos táxons utilizados para representar a subordem e da forma de representação da dieta neste trabalho sugere que a não-identificação de uma influência da dieta na integração neste trabalho seja devida à inclusão de número relativamente reduzido de táxons com dietas distintas (12 feliformia incluídos, entre os quais 6 foram considerados carnívoros estritos e somente 3 não são primariamente carnívoros). A importância da dieta para a evolução da morfologia craniana em Carnivora é mostrada claramente por diversos estudos focados nas médias dos caracteres, ainda que estas relações não sejam necessariamente claras e únicas para as diferentes famílias do grupo (Radinsky 1981a, b; Wroe & Milne, 2007; Goswami et al, 2011).

A importância geral do fator dieta para a evolução do crânio em Carnivora e mamíferos em geral, bem como a fundamentação teórica exposta acima, dão suporte a

uma hipótese prévia de que a dieta potencialmente afete os padrões de integração em Feliformia..

Sem hipótese *a priori*: Os pontos expostos acima mostram claramente que a dieta pode influenciar a estruturação da covariação morfológica craniana. Considerando, como já mencionado, que a magnitude de integração se relaciona fortemente à variação de tamanho, e assim principalmente ao crescimento somático (Hallgrímsson *et al*, 2007; Porto *et al*, 2013), efeitos da dieta sobre a magnitude de integração seriam esperados se levassem a uma alteração nesta última parte do desenvolvimento. Sabe-se que o processo de crescimento somático produz covariação geral no crânio como um todo, mas não de forma isométrica (Hallgrímsson *et al*, 2007). A região da face, que inclui as sub-regiões envolvidas na obtenção de alimento e mastigação (oral e zigomática), cresce mais durante a etapa de crescimento somático em mamíferos (Moore, 1981; Cheverud, 1995), tendendo assim a mostrar alometria positiva. Portanto, é possível que pressões seletivas relacionadas à dieta levem a alterações na integração das sub-regiões funcionalmente importantes para obter e processar alimento por meio de alterações na proporção de tamanho alométrico, resultando assim em mudanças associadas na magnitude geral de integração.

Por outro lado, como explicitado acima, a dieta pode afetar a evolução da morfologia média sem levar a mudanças associadas na integração. Além disso, pressões relacionadas à dieta podem afetar os padrões de integração, mas não as magnitudes de integração, se afetarem aspectos do desenvolvimento não relacionados ao crescimento somático. Os dois trabalhos já realizados que avaliaram influências da dieta sobre a magnitude de integração (Hubbe, 2013; Rossoni, 2013) não encontraram relações entre estas características.

De acordo com o exposto acima, apesar de haver uma possibilidade teórica de a dieta influenciar a evolução das magnitudes de integração, não há razão suficiente para propor um hipótese *a priori* sobre a existência dessas relações em Feliformia. Assim,, as análises de relação dieta x magnitude foram realizadas aqui de forma exploratória.

f) Socialidade

Hipótese: Variações nos comportamentos sociais tendem a se relacionar a diferenças nos padrões de integração principalmente na região do neurocrânio (subregiões da abóboda craniana e do basicrânio).

A hipótese do cérebro social (*social brain hypothesis* - Dunbar, 1988) propõe a existência de uma relação geral entre tamanho do cérebro e grau de socialidade entre mamíferos. Apesar de a validade desta hipótese em Carnivora ter sido questionada por Finarelli & Flynn (2009) estudos mais recentes parecem revalidá-la para mamíferos como um todo (Schultz & Dunbar, 2010) e especificamente para Carnivora, ao menos para alguns aspectos da socialidade (Smith *et al*, 2012). Esta hipótese trata mais diretamente sobre a forma média do cérebro, propondo que espécies mais sociais tenderiam a ter cérebros maiores. Entretanto, devido à relevância do crescimento do cérebro no processo de crescimento e desenvolvimento da abóboda craniana e do basicrânio (Moore, 1981; Cheverud, 1995) é plausível imaginar que os efeitos de pressões seletivas ligadas à socialidade reflitam-se também na forma média do crânio e na integração morfológica das regiões mais diretamente afetadas pelo crescimento do cérebro durante o desenvolvimento(neurocrânio). Sendo assim, considera-se aqui como hipótese prévia a existência de associação entre a evolução dos padrões de integração morfológica e a socialidade. Espera-se, também, maior correlação entre a socialidade e padrões de resposta a seleção caráter-específicos (SRD - Marroig *et al*, 2011) para caracteres da região do neurocrânio.

Sem hipótese *a priori*: Apesar da relação entre socialidade e tamanho do cérebro possivelmente levar a uma maior integração na região do neurocrânio, isso não necessariamente implicaria também aumentos na magnitude total de integração, uma vez que a magnitude de integração se relaciona principalmente à variação no tamanho corpóreo e, assim, é provavelmente mais afetada pela etapa de crescimento somático que pelo crescimento do cérebro (Hallgrímsson, 2007; Porto *et al*, 2013). *Trade-offs* entre o crescimento do cérebro e o crescimento somático durante o desenvolvimento poderiam, talvez, causar efeitos indiretos da socialidade sobre a magnitude de integração. Este tipo de efeito, entretanto, não foi encontrado em um estudo que analisou os efeitos do crescimento cerebral em mamíferos (Barton & Capellini, 2011). Considera-se aqui, portanto, que não há fundamentação teórica suficiente para uma

hipótese prévia quanto à relação entre socialidade e magnitude de integração, de forma que esta análise é realizada aqui de forma exploratória.

Referências

- Abdi, H. 2007. The RV coefficient and the congruence coefficient. *In*: Salkind N. (ed), *Encyclopaedia of Measurement and Statistics*. Sage, Thousand Oaks, CA.
- Adams, D.C. 2015. Evaluating Modularity in Morphometric Data: Challenges with the RV Coefficient and a New Test Measure. *Methods in Ecology and Evolution*: DOI: 10.1111/2041-210X.12511
- Adams, D.C.; Rohlf, J.; Slice, D.E. 2004. Geometric Morphometrics: Ten Years of Progress Following the 'Revolution'. *Italian Journal of Zoology* 71: 5-16.
- Agnarsson, I.; Kuntner, M.; May-Collado, L.J. 2010. Dogs, cats, and kin: A molecular species-level phylogeny of Carnivora. *Molecular Phylogenetics and Evolution* 54:726-745.
- Airoidi, J-P; Flury, B.D. 1988. An application of common principal components analysis to cranial morphometry of *Microtus californicus* and *M. ochrogaster* (Mammalia, Rodentia). *Journal of Zoology* 216: 21-36.
- Albignac, R. 1974. Observations eco-ethologiques sur le genre Eupleres, viverride de Madagascar. *La Terre et la Vie, Revue d'Ecologie Appliquée* 28: 321-351
- Arnold, S.J.; Burger, R.; Hohenlohe, P.A.; Ajie, B.C.; Jones, A.G. 2008. Understanding the evolution and stability of the G-matrix. *Evolution* 62(10): 2451-2461.
- Assis, A.P.A.; Costa, B.M.A.; Rossoni, D.M.; Melo, D.; Marroig, G. 2016. Modularity and Integration. *In*: Kliman, R.M. (ed), *Encyclopedia of Evolutionary Biology* vol. 3 pp. 34-40. Oxford: Academic Press.
- Bailey, I.; Myatt, J.P.; Wilson, A.M. 2013. Group hunting within the Carnivora: physiological, cognitive and environmental influences on strategy and cooperation. *Behavioural Ecology and Sociobiology* 67:1-17.
- Barton, R.A.; Capellini, I. 2011. Maternal investment, life histories, and the costs of brain growth in mammals. *Proceedings of the National Academy of Sciences* 108(15): 6169-6174.
- Barycka, E. 2007. Evolution and systematics of the feliform Carnivora. *Mammalian Biology* 72(5):157-282.
- Beldade, P.; Brakefield, P.M.; Long, A.D. 2005. Generating phenotypic variation: prospects from "evo-devo" research on *Bicyclus anynana* wing patterns. *Evolution & Development* 7(2): 101-107
- Berg, R.L. 1960. The Ecological Significance of Correlation Pleiades. *Evolution* 14(2): 171-180
- Bolstad, G.H.; Hansen, T.F.; Pélabon, C.; Falahati-Anbara, M.; Pérez-Barrales, R.; Armbruster, W.C. 2014. Genetic constraints predict evolutionary divergence in *Dalechampia* blossoms. *Philosophical Transactions of the Royal Society B* 369: DOI: 10.1098/rstb.2013.0255
- Bonnin, I.; Prosperi, J.M.; Olivieri, I. 1997. Comparison of quantitative genetic parameters between two natural populations of a selfing plant species, *Medicago truncatula*. *Theoretical and Applied Genetics* 94: 641-651.
- Burt, C. 1948. Factor analysis and canonical correlations. *British Journal of Psychology* 1: 95-106.
- Cardini, A.; Polly, P.D. 2013. Larger mammals have longer faces because of size-related constraints on skull form. *Nature communications* 4: 2458.
- Charles-Dominique, P. 1978. Ecologie et vie sociale de *Nandinia binotata* (carnivores, viverrides): comparaison avec les prosimiens sympatriques du Gabon. *Terre Vie (Revue d'Ecologie)* 32: 477-528.
- Cheverud, J.M. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. *Evolution* 36(3): 499-516.
- Cheverud, J.M. 1984. Quantitative genetics and developmental constraints on evolution by selection. *Journal of theoretical biology* 110(2): 155-171
- Cheverud, J.M. 1988. A comparison of genetic and phenotypic correlations. *Evolution* 42: 958-968
- Cheverud, J.M. 1995. Morphological Integration in the Saddle-Back Tamarin (*Saguinus fuscicollis*) Cranium. *The American Naturalist* 145(1): 63-89.
- Cheverud, J.M. 1996b. Developmental integration and the evolution of pleiotropy. *American Zoologist* 36: 44-50.
- Cheverud, J.M. 1996a. Quantitative genetic analysis of cranial morphology in the cotton-top

- (*Saguinus oedipus*) and saddle-back (*Saguinus fuscicollis*) tamarins.
- Cheverud, J.M. 2004. Modular pleiotropic effects of quantitative trait loci on morphological traits. *In*: Schlosser, G.; Wagner, G.P. (eds) *Modularity in Development and Evolution*, 1st ed. Chicago, IL: The University of Chicago Press, pp. 132-153.
- Cheverud, J.M.; Marroig, G. 2007. Comparing covariance matrices: random skewers method compared to the common principal components model. *Genetics and Molecular Biology* 30(2): 461-469.
- Christiansen, P. 2008a. Evolution of skull and mandible shape in cats (Carnivora: Felidae). *PloS one* 3(7): e2807
- Christiansen, P. 2008b. Evolutionary changes in craniomandibular shape in the great cats (*Neofelis* Griffith and *Panthera* Oken). *Biological Journal of the Linnean Society* 95: 766-778.
- Christiansen, P.; Wroe, S. 2007. Bite forces and evolutionary adaptations to feeding ecology in carnivore. *Ecology* 88: 347-358.
- Costa, B.M.A. 2013. Evolução e integração morfológica do crânio dos roedores da subfamília Sigmodontinae Wagner, 1843 (Rodentia, Cricetidae). Tese de Doutorado, Universidade de São Paulo.
- Crawford-Cabral, J. 1981. The classification of the genets (Carnivora, Viverridae, genus *Genetta*). *Boletim da Sociedade Portuguesa de Ciências Naturais* 20: 97-114.
- Crawford-Cabral, J. 1993. A comment on the systematic position of *Poiana*. *Small Carnivore Conservation* 9:8.
- Crow, J.F.; Kimura, M. 1970. *An introduction to population genetics theory*. New York: Evanston and London: Harper & Row.
- Darwin, C. 1859. *On the Origin of Species by Natural Selection*. London: J. Murray.
- Davis, D.D. 1958. Mammals of the Kelabit Plateau northern Sarawak. *Fieldiana Zoology* 39: 119-147.
- De Conto, V. 2007. *Genética quantitativa e evolução morfológica em Akodon cursor*. Tese de doutorado, Universidade Federal do Rio de Janeiro, RJ.
- Driscoll, C.A.; Menotti-Raymond, M.; Roca, A.L.; Hupe, K.; Johnston, W.E.; Geffen, E.; Harley, E.H.; Delibes, M.; Pontier, D.; Kitchener, A.C.; Yamaguchi, N.; O'Brien, S.J.; Macdonald, D.W. 2007. The Near Eastern Origin of Cat Domestication. *Science* 317: 519-523.
- Durbin, J.; Funk, S.M.; Hawkins, F.; Hills, D.M.; Jenkins, P.D.; Moncrieff, C.B.; Ralainasolo, F.B. 2010. Investigations into the status of a new taxon of *Salanoia* (Mammalia: Carnivora: Eupleridae) from the marshes of Lac Alaotra, Madagascar. *Systematics and Biodiversity* 8(3): 341-355.
- Eizirik, E.; Murphy, W.J.; Koepfli, K.-P.; Johnson, W.E.; Dragoo, J.W.; Wayne, R.K.; O'Brien, S.J. 2010. Pattern and timing of diversification of the mammalian order Carnivora inferred from multiple nuclear gene sequences. *Molecular Phylogenetics and Evolution* 56:49-63.
- Falconer, D.S.; Mackay, T.F.C. 1996. *Introduction to quantitative genetics*. 4th edition. Harlow, UK: Longman
- Felsenstein, J. 1988. Phylogenies and quantitative characters. *Annual Review of Ecology and Systematics* 19: 445-471.
- Ferretti, M.P. 2007. Evolution of bone-cracking adaptations in hyaenids (Mammalia, Carnivora). *Swiss journal of geosciences* 100:41-52.
- Figueirido, B.; Serrano-Alarcón F.J.; Slater, G.J.; Palmqvist, P. 2010. Shape at the crossroads: homoplasy and history in the evolution of the carnivoran skull towards herbivory. *J. Evol. Biol* 23: 2579-2594
- Finarelli, J.A.; Flynn, J.J. 2009. Brain-size evolution and sociality in Carnivora. *PNAS* 106(23): 9345-9349.
- Fisher, R.A. 1922. On the dominance ratio. *Proceedings of the Royal Society of Edinburgh* 42: 321-341.
- Fisher, R.A. 1930. The distribution of gene ratios for rare mutations. *Proceedings of the Royal Society of Edinburgh* 50: 204-219.
- Flynn, J.J.; Finarelli, J.A.; Zehr, S.; Hsu, J.; Nedbal, M.A. 2005. Molecular phylogeny of the Carnivora (Mammalia): assessing the impact of increased sampling on resolving enigmatic relationships. *Systematic Biology* 54: 317-337.
- Flynn, J.J.; Nedbal, M.A. 1998. Phylogeny of the Carnivora (Mammalia): Congruence vs incompatibility among multiple data sets. *Molecular Phylogenetic Evolution* 9:414-426.
- Garcia, G.; Hingst-Zaher, E.; Cerqueira, R.; Marroig, G. 2014. Quantitative Genetics and Modularity in Cranial and Mandibular Morphology of *Calomys expulsus*. *Evolutionary Biology* 41(4): 619-636.
- Garcia, G.; Oliveira, F.B.; Marroig, G. *in prep*. Modularity and Morphometrics: Error Rates in Hypothesis Testing. Disponível no BioRxiv. doi: <http://dx.doi.org/10.1101/030874>.

- Gaubert, P.; Fernandes, C.A.; Bruford, M.W.; Veron, G. 2004a. Genets (Carnivora, Viverridae) in Africa: An evolutionary synthesis based on cytochrome b sequences and morphological characters. *Biological Journal of the Linnean Society* 81:589-610.
- Gaubert, P.; Taylor, P.J.; Fernandes, C.A.; Bruford, M.W.; Veron, G. 2005b. Patterns of cryptic hybridization revealed using an integrative approach: a case study on genets (Carnivora, Viverridae, *Genetta* spp.) from the southern African subregion. *Biological Journal of the Linnean Society* 86: 11-33.
- Gaubert, P.; Tranier, M.; Delmas, A.-S.; Colyn, M.; Veron, G. 2004b. First molecular evidence for reassessing phylogenetic affinities between genets (*Genetta*) and the enigmatic genet-like taxa *Osbornictis*, *Poiana* and *Prionodon* (Carnivora, Viverridae). *Zool. Scr.* 33: 117-129.
- Gaubert, P.; Veron, G. 2003. Exhaustive sample set among Viverridae reveals the sister-group of felids: The linsangs as a case of extreme morphological convergence within Feliformia. *Proceedings of the Royal Society of London: Biological Sciences* 270:2523-2530.
- Gaubert, P.; Wozencraft, W.C.; Cordeiro-Estrela, P.; Veron, G. 2005a. Mosaics of Convergences and Noise in Morphological Phylogenies: What's in a Viverrid-Like Carnivoran? *Systematic Biology* 54(6): 865-894.
- Goodman, S.M.; Helgen, K.M. 2010. Species limits and distribution of the Malagasy carnivoran genus *Eupleres* (Family Eupleridae). *Mammalia* 74: 177-185.
- Goswami, A. 2006a. Morphological integration in the carnivoran skull. *Evolution* 60 (1): 169-183.
- Goswami, A. 2006b. Cranial Modularity Shifts during Mammalian Evolution. *The American Naturalist* 168(2): 270-280.
- Goswami, A.; Polly, P.D. 2010. The influence of modularity on cranial morphological disparity in Carnivora and Primates (Mammalia). *PloS One* 5(3).
- Goswami, A.; Milne, N.; Wroe, S. 2011. Biting through constraints: cranial morphology, disparity and convergence across living and fossil carnivorous mammals. *Proceedings of the Royal Society B: Biological Sciences* 278: 1831-1839. doi: 10.1098/rspb.2010.2031
- Gregory, W.K.; Hellman, M. 1939. On the evolution and major classification of the civets (Viverridae) and allied fossil and recent Carnivora: a phylogenetic study of the skull and dentition. *Proceedings of the American Philosophical Society* 81: 309-392.
- Haber, A. 2011. A comparative analysis of integration indices. *Evolutionary Biology* 38: 476-488.
- Haber, A. 2015. The Evolution of Morphological Integration in the Ruminant Skull. *Evolutionary Biology* 42: 99-114.
- Hallgrímsson, B.; Jamniczky, H.; Young, N.; Rolian, C.; Parsons, T.; Boughner, J.; Marcucio, R. 2009. Deciphering the palimpsest: studying the relationship between morphological integration and phenotypic covariation. *Evolutionary Biology* 36(4): 355-376
- Hallgrímsson, B.; Lieberman, D.E.; Young, N.M.; Parsons, T.; Wat, S. 2007. Evolution of covariance in the mammalian skull. *Novartis Foundation Symposium* 284: 164-190.
- Hansen, T.; Houle, D. 2008. Measuring and comparing evolvability and constraint in multivariate characters. *Journal of Evolutionary Biology*, 21(5): 1201-1219
- Holekamp, K.E.; Dantzer, B.; Stricker, G.; Yoshida, K.C.S.; Benson-Amram, S. 2015. Brains, brawns and sociality: a hyaena's tale. *Animal Behaviour* 103: 237-248.
- Holekamp, K.E.; Smith, J.E.; Strelhoff, C.C.; Van Horn, R.C.; Watts, H.E. 2012. Society, demography and genetic structure in the spotted hyena. *Molecular Ecology* 21: 613-632.
- Holliday, J.; Steppan, S. 2004. Evolution of hypercarnivory: the effect of specialization on morphological and taxonomic diversity. *Paleobiology* 30(1): 108-128.
- Hotelling, H. 1936. Relations between two sets of variates. *Biometrika* 28: 321.
- Hubbe, A. 2013. Análise morfológica craniana de *Xenarthra* atuais e extintos: inferências evolutivas e funcionais. Tese de Doutorado, Universidade de São Paulo.
- Janečka, J.E.; Walker, C.W.; Tewes, M.E.; Caso, A.; Laack, L.L.; Honeycutt, R.L. 2007. Phylogenetic relationships of ocelot (*Leopardus pardalis albescens*) populations from the Tamaulipan Biotic Province and Implications for Recovery. *The Southwestern Naturalist* 52(1): 89-96.
- Joeckel, R.M. 1998. Unique frontal sinuses in fossil and living Hyaenidae (Mammalia, Carnivora): description and interpretation. *Journal of Vertebrate Paleontology* 18: 627-639.
- Johnson, W.E.; Eizirik, E.; Pecon-Slattery, J.; Murphy, W.J.; Antunes, A.; Teeling, E.; O'Brien, S.J. 2006. The Late Miocene Radiation of Modern Felidae: A Genetic Assessment. *Science* 311(5757): 73-77

- Jolicoeur, P. 1963. The Multivariate Generalization of the Allometry Equation. *Biometrics* 19: 497-499.
- Kimura, M. 1968a. Evolutionary Rate at the Molecular Level. *Nature* 217: 624-626.
- Kimura, M. 1968b. Genetic variability maintained in a finite population due to mutational production of neutral and nearly neutral isoalleles. *Genetical Research* 11(3): 247-269.
- Kimura, M. 1970. Preponderance of synonymous changes as evidence for the neutral theory of molecular evolution. *Nature* 227: 275-276.
- Klingenberg, C. 2008. Morphological integration and developmental modularity. *Annual Review of Ecology, Evolution and Systematics* 39: 115-132.
- Klingenberg, C.P. 2014. Studying morphological integration and modularity at multiple levels: concepts and analysis. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 369 (1649) doi: 10.1098/rstb.2013.0249
- Koepfli, K-P.; Jenks, S.M.; Eizirik, E.; Zahirpour, T.; Van Valkenburgh, B.; Wayne, R.K. 2006. Molecular systematics of the Hyaenidae: Relationships of a relictual lineage resolved by a molecular supermatrix.
- Koots, K.R.; Gibson, J.P. 1996. Realized sampling variances of estimates of genetic parameters and the difference between genetic and phenotypic correlations. *Genetics* 143: 1409-1416.
- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution* 33(1): 402-416.
- Lande, R. 1980. The genetic covariance between characters maintained by pleiotropic mutations. *Genetics* 94: 203-215
- Lewontin, R. 1974. *The Genetic Basis of Evolutionary Change*. Columbia University Press
- Li, G.; Davis, B.W.; Eizirik, E.; Murphy, W.J. 2016. Phylogenomic evidence for ancient hybridization in the genomes of living cats (Felidae). *Genome Research* 26(1): 1-11. doi: 10.1101/gr.186668.114.
- Lim, B.L. 1973. The banded linsang and the banded musang of West Malaysia. *Malay Nat J* 26:105-111.
- Linde, K. van der; Houle, D. 2009. Inferring the Nature of Allometry from Geometric Data. *Evolutionary Biology* 36: 311-322.
- Lipson, H.; Pollack, J.B.; Suh, N.P. 2002. On the origin of modular variation. *Evolution* 56(8): 1549-1556.
- Lock, R.H. 1906. *Recent Progress in the Study of Variation, Heredity and Evolution*. London and New York
- Lynch, M.; Walsh, B. 1997. *Genetics and analysis of quantitative traits*. Sinauer Associates Incorporated
- Macdonald, D.W.; Yamaguchi, N.; Kerby, G. 2000. Group-living in the domestic cat: its sociobiology and epidemiology. In: *The Domestic Cat: The Biology of Its Behaviour*. Turner, D.C. Cambridge University Press. pp 95-118.
- Marroig, G.; Cheverud J.M.. 2001. A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology, and ontogeny during cranial evolution of new world monkeys. *Evolution* 55(12): 2576-600.
- Marroig, G.; Cheverud J.M.. 2005 Size as a line of least evolutionary resistance: diet and adaptive morphological radiation in New World monkeys. *Evolution* 59(5): 1128-42
- Marroig, G.; Cheverud, J. 2010. Size as a line of least resistance II: direct selection on size or correlated response due to constraints? *Evolution* 64(5): 1470-1488.
- Marroig, G.; Shirai, L.T.; Porto, A.; Oliveira, F.B.; Conto, V. 2009. The evolution of modularity in the mammalian skull II: Evolutionary consequences. *Evolutionary Biology* 36(1): 136-148
- Marroig, G.; Melo, D.; Porto, A.; Sebastião, H.; Garcia, G. 2011. Selection Response Decomposition (SRD): A New Tool for Dissecting Differences and Similarities Between Matrices. *Evolutionary Biology* 38: 225-241.
- Martin, L.D. 1989. Fossil history of terrestrial carnivora. In: Gittleman, J.L. ed. *Carnivore behaviour, ecology, and evolution*. New York, NY: Cornell University Press: 536-568.
- Martínez-Abadías, N.; Esparza, M.; Sjøvold, T.; González-José, R.; Santos, M.; Hernández, M.; Klingenberg, C.P. 2011. Pervasive Genetic Integration Directs the Evolution of Human Skull Shape. *Evolution* 66(4): 1010-1023.
- Martín-Serra, A.; Figueirido, B.; Pérez-Claros, J.A.; Palmqvist, P. 2015. Patterns of morphological integration in the appendicular skeleton of mammalian carnivores. *Evolution* 69(2): 321-340.
- Mattern, M.Y.; McLennan, D.A. 2000. Phylogeny and Speciation of Felids. *Cladistics* 16(2): 232-253.

- Meachen-Samuels, J.; van Valkenburgh, B. 2009. Craniodental indicators of prey size preference in the Felidae. *Biological Journal of the Linnean Society* 4: 784-799.
- Meiri, S.; Dayan, T.; Simberloff, D. 2005. Variability and correlations in carnivore crania and dentition. *Functional Ecology* 2: 337-343
- Meloro, C.; Slater, G.J. 2012. Covariation in the skull modules of cats: the challenge of growing saber-like canines. *Journal of Vertebrate Paleontology* 32(3): 677-685.
- Monteiro, L.R.; Nogueira, M.R. 2009. Adaptive radiations, ecological specialization, and the evolutionary integration of complex morphological structures. *Evolution* 64(3): 724-744.
- Moore, W.J. 1981. *The mammalian skull*. Cambridge: Cambridge University Press.
- Nascimento, F.O. 2010. Revisão taxonômica do gênero *Leopardus* Gray, 1842 (Carnivora, Felidae). Tese de Doutorado, Instituto de Biociências, Universidade de São Paulo.
- Nowak R.M. 1999. *Walker's mammals of the world*. Volume 1 & 2. Johns Hopkins University Press, Baltimore.
- Nyakatura, K.; Bininda-Emonds, O.R.P. 2012. Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. *BMC Biology* 10(12): doi:10.1186/1741-7007-10-12
- Oliveira, F.B.; Porto, A.; Marroig, G. 2009. Covariance structure in the skull of Catarrhini: a case of pattern stasis and magnitude evolution. *Journal of Human Evolution* 56(4): 417-430.
- Olson, E.V.; Miller, R. 1958. *Morphological Integration*. Chicago: University of Chicago Press
- Olson, E.V.; Miller, R.L. 1951. A mathematical model applied to a study of the evolution of species. *Evolution* 5(4): 325-338
- Patou, M.-L.; Mclenachan, P.A.; Morley, C.G.; Couloux, A.; Jennings, A.P.; Veron, G. 2009. Molecular phylogeny of the Herpestidae (Mammalia, Carnivora) with a special emphasis on the Asian Herpestes. *Molecular Phylogenetics and Evolution* 53: 69-80.
- Patou, M.-L.; Wilting, A.; Gaubert, P.; Esselstyn, J.A.; Cruaud, C.; Jennings, A.P.; Fickel, J.; Veron, G. 2010. Evolutionary history of the *Paradoxurus* palm civets - a new model for Asian biogeography. *Journal of Biogeography* 37(11): 2077-2097
- Patou, M.-L.; Debruyne, R.; Jennings, A.P.; Zubaid, A.; Rovie-Ryan, J.J.; Veron, G. 2008. Phylogenetic relationships of the Asian palm civets (Hemigalinae & Paradoxurinae, Viverridae, Carnivora). *Molecular Phylogenetics and Evolution* 47: 883-892.
- Pavlicev, M.; Cheverud, J.M.; Wagner, G.P. 2009b. Measuring morphological integration using eigenvalue variance. *Evolutionary Biology* 36(1): 157-170
- Pavlicev, M.; Cheverud, J.M.; Wagner, G.P. 2011b. Evolution of adaptive phenotypic variation patterns by direct selection for evolvability. *Proceedings of the Royal Society* 278(1713): 1903-1912.
- Pavlicev, M.; Norgard, E.A.; Fawcett, G.L.; Cheverud, J.M. 2011. Evolution of pleiotropy: Epistatic interaction pattern supports a mechanistic model underlying variation in genotype-phenotype map. *Journal of Experimental Zoology B* 316 (5): 371-385.
- Pavlicev, M.; Wagner, G.; Cheverud, J.M. 2009a. Measuring evolutionary constraints through the dimensionality of the phenotype: Adjusted bootstrap method to estimate rank of phenotypic covariance matrices. *Evolutionary Biology* 36(3): 339-353.
- Perez, M.; Li, B.; Tillier, A.; Cruaud, A.; Veron, G. 2006. Systematic relationships of the bush-tailed and black-footed mongooses (genus *Bdeogale*, Herpestidae, Carnivora) based on molecular, chromosomal and morphological evidence. *Journal Zool Syst and Evol Research* 44(3): 251-259.
- Phang-Chong-Ahn. 1980. Morphology and ecology of Viverridae in Vietnam. *Zool Zh* 59: 905-914.
- Polly, P.D. 2008. Developmental dynamics and G-Matrices: Can Morphometric Spaces be used to model phenotypic evolution? *Evolutionary Biology* 35(2): 83-96
- Porto, A.; Oliveira, F.B.; Shirai, L.T.; de Conto, V.; Marroig, G. 2009. The Evolution of Modularity in the Mammalian Skull I: Morphological Integration Patterns and Magnitudes. *Evolutionary Biology* 36:118-135.
- Porto, A.; Shirai, L.T.; Oliveira, F.B.; Marroig, G. 2013. Size variation, growth strategies and the evolution of modularity in the mammalian skull. *Evolution* 67(11): 3305-3322
- Rapson, S.A.; Goldizen, A.W.; Seddon, J.M. 2012. Species boundaries and possible hybridization between the black mongoose (*Galerella nigrata*) and the slender mongoose (*Galerella sanguinea*). *Molecular Phylogenetics and Evolution* 65: 831-839.
- Reusch, T.; Blanckenhorn, W.U. 1998. Quantitative genetics of the dung fly *Sepsis*

- cynipsea: Cheverud's conjecture revisited. *Heredity* 81: 111-119.
- Richardson, P.R.K. 1988. Mate desertion in response to female promiscuity in the socially monogamous aardwolf, *Proteles cristatus*. *South African Journal of Zoology* 23: 306-308.
- Roff, D.A. 1995. The estimation of genetic correlations from phenotypic correlations: a test of Cheverud's conjecture. *Heredity* 74: 481-490.
- Roff, D.A. 1996. The evolution of genetic correlations: an analysis of patterns. *Evolution* 50: 1392-1403.
- Roff, D.A. 1997. *Evolutionary quantitative genetics*. New York: Chapman & Hall.
- Roff, D.A. 2000. The evolution of the G matrix: Selection or drift? *Heredity* 84(2): 135-142.
- Rossoni, D.M. 2013. Integração morfológica craniana em morcegos da Família Phyllostomidae. Tese de Doutorado, Universidade de São Paulo.
- Sakamoto, M.; Ruta, M. 2012. Convergence and Divergence in the Evolution of Cat Skulls: Temporal and Spatial Patterns of Morphological Diverity. *PLoS ONE* 7(7): e39752.
- Schluter, D. 1996. Adaptive Radiation along Genetic Lines of Least Resistance. *Evolution* 50(5): 1766-1774.
- Shirai, L.T.; Marroig, G. 2010. Skull modularity in neotropical marsupials and monkeys: size variation and evolutionary constraint and flexibility. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 314B(8): 663-683.
- Sicuro, F.L. 2011. Evolutionary trends on extant cat skull morphology (Carnivora: Felidae): a three-dimensional geometrical approach. *Biological Journal of the Linnean Society* 103: 176-190.
- Sicuro, F.L.; Oliveira, L.F.B. 2011. Skull morphology and functionality of extant Felidae (Mammalia: Carnivora): a phylogenetic and evolutionary perspective. *Zoological Journal of the Linnean Society* 161: 414-462.
- Simons, A.; Roff, D.A. 1996. The effect of a variable environment on the genetic correlation structure in a field cricket. *Evolution* 50: 267-275.
- Slater, G.J.; Van Valkenburgh B. 2008. Long in the tooth: evolution of sabertooth at cranial shape. *Paleobiology* 34:403-419.
- Slater, G.J.; Van Valkenburgh, B. 2009. Allometry and performance: the evolution of skull form and function in felids. *Journal of Evolutionary Biology* 22: 2278-2287.
- Smith, J.E.; Swanson, E.M.; Reed, D.; Holekamp, K.E. 2012. Evolution of Cooperation among Mammalian Carnivores and its Relevance to Hominin Evolution. *Current Anthropology* 53(S6): S436-S452.
- Smith, K.K. 1997. Comparative patterns of craniofacial development in Eutherian and Metatherian mammals. *Evolution* 51(5): 1663-1678.
- Sonet, G.; Colyn, M.; Verheyen, E.; Nagy, Z.T.; Wendelen, W.; van Rompaey, H.; Hulselmans, J. 2014. Afrotropical forest-dwelling mongooses (Mammalia: Herpestidae: *Crossarchus*) investigated by craniometry and mitochondrial DNA. *Journal Zool Syst and Evol Research*: doi: 10.1111/jzs.12066.
- Stalker, H.D.; Carson, H.L. 1947. Morphological variation in natural populations of *Drosophila robusta* Sturtevant. *Evolution* 1(4): 237-248.
- Steppan, S.J. 1997a. Phylogenetic analysis of phenotypic covariance structure. I. Contrasting results from matrix correlation and common principal component analysis. *Evolution* 51(2): 571-586.
- Steppan, S.J. 1997b. Phylogenetic analysis of phenotypic covariance structure. II. Reconstructing Matrix Evolution. *Evolution* 51(2): 587-594.
- Steppan, S.J.; Phillips, P.C.; Houle, D. 2002. Comparative quantitative genetics: Evolution of the G-matrix. *Trends in Ecology & Evolution* 17(7): 320-327.
- Tapadia, M.D.; Cordero, D.R.; Helms, J.A. 2005. It's all in your head: new insights into craniofacial development and deformation. *Journal of Anatomy* 207 (5): 461-477.
- Teissier, G. 1960. Relative growth. In: *The physiology of crustacea. I. Metabolism and growth*. T. H. Waterman (ed.) Academic Press, New York. pp 537-560.
- Terentjev, P.V. 1931. Biometrische Untersuchungen über die morphologischen Merkmale von *Rana ridibunda* Pall. (Amphibia, Salientia). *Biometrika* 23: 23-51.
- Trigo, T.C.; Schneider, A.; Oliveira, T.G.; Lehugeur, L.M.; Silveira, L.; Freitas, T.R.O.; Eizrik, E. 2013. Molecular Data Reveal Complex Hybridization and a Cryptic Species of Neotropical Wild Cat. *Current Biology* 23: 1-6.
- Tseng, Z.J.; Wang, X. 2011. Do convergent ecomorphs evolve through convergent morphological pathways? Racial shape evolution in fossil hyaenids and borophagine canids (Carnivora, Mammalia). *Paleobiology* 37(3): 470-489.

- Tucic, B.; Avramov, S. 1996. Morphological integration in the seedlings of *Iris pumila*. *Genetika* 32: 1235-1242.
- Tucker, L.R. 1951. A method for the synthesis of factor analysis studies (Personnel Research Section Report No 984). Washington: Department of the Army.
- Van Valen, L.M. 1974. Multivariate structural statistics in natural history. *Journal of Theoretical Biology* 45: 235-247.
- Van Valkenburgh, B. 1988. Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology* 14(2): 155-173.
- Van Valkenburgh, B. 2007. Déjà vu: the evolution of feeding morphologies in the Carnivora. *Integrative and Comparative Biology* 47(1): 147-163.
- Vermeij, G.J. 1973. Adaptation, versatility, and evolution. *Systematic Zoology* 22: 466-477.
- Veron, G.; Catzeflis, F. 1993. Phylogenetic relationships of the endemic Malagasy Carnivore *Cryptoprocta ferox* (Aeluroidea): DNA/DNA hybridization experiments. *Journal of Mammalian Evolution* 1: 169-185.
- Veron, G.; Colyn, M.; Dunham, A.E.; Taylor, P.; Gaubert, P. 2004. Molecular systematics and origin of sociality in mongooses (Herpestidae, Carnivora). *Molecular Phylogenetics and Evolution* 30: 582-598.
- Veron, G.; Heard, S. 2000. Molecular systematics of the Asiatic Viverridae (Carnivora) inferred from mitochondrial cytochrome b sequence analysis. *Journal Zool. Syst. Evol. Res.* 38:209-217.
- Veron, G.; Patou, M.-L.; Debruyne, R.; Couloux, A.; Fernandez, D.A.P.; Wong, S.T.; Fuchs, J.; Jennings, A.P. 2015b. Systematics of the Southeast Asian mongooses (Herpestidae, Carnivora): solving the mystery of the elusive collared mongoose and Palawan mongoose. *Zoological Journal of the Linnean Society* 173: 236-248.
- Veron, G.; Patou, M.-L.; Jennings, A.P. 2015a. Molecular systematics of the small-toothed palm civet (*Arctogalidia trivirgata*) reveals a strong divergence of Borneo populations. *Mammalian Biology* 80(40): 347-354.
- Veron, G.; Patou, M.-L.; Tóth, M.; Goonatilake, M.; Jennings, A.P. 2014. How many species of *Paradoxurus* civets are there? New insights from India and Sri Lanka. *Journal Zool Syst and Evol Research* 53(2): 161-174.
- Wagner, G. P. 1984. On the eigenvalue distribution of genetic and phenotypic dispersion matrices: Evidence for a nonrandom organization of quantitative character variation. *Journal of Mathematical biology* 21: 77-95.
- Wagner, G.P.; Altenberg, L. 1996. Complex adaptations and the evolution of evolvability. *Evolution* 50(3): 967-976.
- Wagner, G.P.; Pavlicev, M.; Cheverud, J. 2007. The road to modularity. *Nature Reviews Genetics* 8(12): 921-931.
- Wagner, G.P.; Zhang, J. 2011. The pleiotropic structure of the genotype-phenotype map: The evolvability of complex organisms. *Nature Review Genetics* 12 (3): 204-213.
- Waitt, D.E.; Levin, D.A. 1998. Genetic and phenotypic correlations in plants: a botanical test of Cheverud's conjecture. *Heredity* 80: 310-319.
- Werdelin, L. 1983. Morphological patterns in the skulls of cats. *Biological Journal of the Linnean Society* 19: 375-391.
- Werdelin, L.; Solounias, N. 1991. The Hyaenidae: taxonomy, systematics and evolution. *Fossils and Strata* 30: 1-104.
- Wesley-Hunt, G.D.; Flynn, J.J. 2005. Phylogeny of the Carnivora: basal relationships among the Carnivoramorphans and assessment of the position of 'Miacoidea' relative to Carnivora. *Journal of Systematic Palaeontology* 3(3): 1-28.
- West, G.B.; Brown, J.H.; Enquist, B.J. 2001. A general model for ontogenetic growth. *Nature* 413: 628-631.
- Wilting, A.; Buckley-Beason, V.A.; Feldhaar, H.; Gadau, J.; O'Brien, S.J. Linsenmair, K.E. 2007. Clouded leopard phylogeny revisited: support for species recognition and population division between Borneo and Sumatra. *Frontiers in Zoology* 4:15.
- Wilting, A.; Fickel, J. 2012. Phylogenetic relationship of two threatened endemic viverrids from the Sunda Islands, Hose's civet and Sulawesi civet. *Journal of Zoology* 288(3): 184-190.
- Wozencraft, W.C. 1984. A phylogenetic reappraisal of the Viverridae and its relationship to other Carnivora. PhD thesis, University of Kansas, Lawrence, KS.
- Wozencraft, W.C. 1986. A New Species of Striped Mongoose from Madagascar. *Journal of Mammalogy* 67(3): 561-571.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16: 97-159.
- Wroe, S.; Milne, N. 2007. Convergence and remarkably consistent constraint in the evolution of carnivore skull shape. *Evolution* 61(5): 1251-1260.

Yoder, A.D.; Burns, M.M.; Zehr, S.; Delefosse, T.; Veron, G.; Goodman, S.M.; Flynn, J.J. 2003. Single origin of Malagasy Carnivora from an African ancestor. *Nature* 421:734-737.

Zeng, Z.B. 1988. Long-term correlated response, interpopulation covariation and interspecific allometry. *Evolution* 42: 363-374.

Chapter 2: Skull morphological integration and its links to phylogeny, morphology, size and ecology in Feliform Carnivorans (Mammalia: Carnivora: Feliformia)

Abstract

Understanding how morphological integration changes throughout the evolutionary history of a lineage is an important aspect to understand phenotypic evolution. Previous studies in mammals have often found skull morphological integration to be remarkably conservative in terms of patterns (which parts of the skull covary the most), but more variable in magnitude (how correlated is the skull as a whole). Although more conservative, integration patterns show links to phylogeny, morphology and diet in some cases, implying at least some differentiation tied to or influenced by historical and/or ecological factors. Despite the astonishing size, shape, phylogenetic and ecological diversity of feliform Carnivora, investigations of morphological integration in this group have been restricted to a very limited number of species. Here we used the largest database of Feliformia to date to study morphological integration patterns and overall magnitudes of integration for taxa belonging to all seven feliform families. We also calculated the proportion of within-population isometric size variation for different taxa, relating it to overall integration magnitudes. Additionally, we analyse associations between integration patterns and magnitudes and a variety of factors: average size, average morphology, phylogenetic history and two ecological traits (diet and sociality). We show that integration patterns are mostly conserved in Feliformia, as occurs in other groups of mammals, but find some distinction between Felidae, Hyaenidae, Prionodontidae and the remaining families. Integration magnitudes closely mirrored both isometric and allometric size variation, with generally higher values in Felids and low values in *Prionodon* and Hyaenidae, but show variations almost as wide as those found elsewhere between different mammalian orders. Integration patterns were often similar in morphologically convergent taxa, and were also partly followed by magnitudes of integration. In fact, we found a general association among average morphology, patterns and magnitudes of integration within the suborder and some less-inclusive groups. We identified significant phylogenetic signal for integration patterns within most phylogenetic groups above, but few below the family level, indicating that the structuring of morphological integration apparently occurs in large part within families. For Feliformia as a whole, sociality had no effect on covariance patterns, while diet was associated to integration only when not accounting for phylogeny, although the covariance patterns of particular skull characters seem to be affected by dietary differences even after taking into account phylogenetic relatedness. One family in particular (Herpestidae) had integration patterns significantly related to dietary differences and also to sociality, showing for the first time an association between skull morphological integration and social behaviour, possibly reflecting aspects of brain development.

Introduction

Variation has had a central role on evolutionary theory from its very onset. Heritable variation stands at the core of both Darwin's original formulation of evolution by natural selection (Darwin, 1859; Fisher, 1930) and random evolution by Genetic Drift (Wright, 1931), whereas mutation is generally understood in current evolutionary theory as a force which generates new variation (e.g. Cheverud, 1984; Jones *et al*, 2007; but see Nei, 2013). In order to understand the phenotypic evolution of complex morphological structures, an essential aspect is how variation is structured among their various component traits - a concept known as morphological integration (Olson & Miller, 1951, 1958; Cheverud, 1982, 1984; Klingenberg, 2013). Morphological integration lies at the root of Gould & Lewontin (1979)'s second alternative to adaptationist explanations, since changes in the form of a part of an organism may arise from correlated consequences of selection on other parts. This has obvious consequences for microevolutionary changes (Lande, 1979; Lande & Arnold, 1983) and is arguably also important for macroevolution (Lande, 1986; Arnold *et al*, 2001; Hansen & Houle, 2008; Pavlicev *et al*, 2009a; Marroig *et al*, 2009; Bolstad *et al*, 2014).

Multivariate phenotypic evolution is expressed within a quantitative genetics framework using Lande (1979)'s equation of multivariate response to selection: $\Delta z = \mathbf{G}\mathbf{P}^{-1}s$, where $\mathbf{G}$ and $\mathbf{P}$ are within-population genetic and phenotypic covariance (i.e. integration) matrices, respectively, while s and Δz are vectors representing selection differentials and evolutionary responses on each character, respectively. If $\mathbf{P}$ and $\mathbf{G}$ remain reasonably stable relative to among-population divergence (Lande, 1979), or if they can be reconstructed based on a clade's evolutionary history (Haber, 2015), Lande (1979)'s equation may be used to represent macroevolutionary change. Therefore, a central topic for understanding evolution and diversification, both among populations and in macroevolution, is the evolution of integration itself.

Although theoretically the evolution of $\mathbf{G}$ has more straightforward evolutionary relevance, $\mathbf{P}$ has been shown to be evolutionarily meaningful itself (e.g. Burger, 1986; Roff & Mousseau, 2005; Pitchers *et al*, 2013). Moreover, a wealth of evidence supports that the more easily estimated $\mathbf{P}$ matrices are remarkably similar to $\mathbf{G}$ matrices (whose estimation depends on a multitude of individuals with known genealogies), at least for morphological characters (Cheverud, 1988, Roff, 1995; Reusch & Blankenhorn, 1998; Waits & Levin, 1998), and specifically for mammal skulls (Cheverud, 1996a; Porto *et*

al, 2009; Garcia *et al*, 2014). Therefore, **P** matrices may be used as better-estimated substitutes for **G**, facilitating larger-scale comparative studies.

Integration may be studied at different levels of organization (Klingenberg, 2014). The one which has the greatest relevance to understanding the evolution of integration itself, however, is within-population integration/ covariance. This level of integration is estimated after removing external sources of variation such as sexual dimorphism, time, geography and specific/subspecific differences, and is understood to reflect a combination of genetic (i.e. pleiotropy and linkage disequilibrium), functional and developmental factors during development (Olson & Miller, 1951, 1958; Cheverud, 1982, 1984; Hallgrímsson *et al*, 2002, 2007, 2009; Klingenberg, 2008; Armbruster *et al*, 2014). This aspect of integration thus echoes the phenotypic variation present in actual evolving populations, and it is this facet we focus on in this study. A variety of studies focus instead on among-population covariation ("evolutionary integration" - Cheverud, 1996b), based on differences among population means instead of individual values (Monteiro *et al*, 2005; Wroe & Milne, 2007; Monteiro & Nogueira, 2009; Goswami & Polly, 2010a; Carnivora in Drake & Klingenberg, 2010; Meloro & Slater, 2012; Linde-Medina *et al*, 2016). As among-population covariation may arise from coordinated evolution due to shared within-population integration, from similar selection regimes, or from both (Felsenstein, 1988; Zeng, 1988), studies focusing exclusively on among-population covariances cannot distinguish effects of co-selection from those of integration-related constraints.

Previous studies dealing with the evolution of (within-population) **G** and **P** along the last decades have revealed a complex scenario. That integration can evolve is shown by multiple theoretical and simulation studies, under different conditions (Turelli, 1988; Roff, 2000; Steppan *et al*, 2002; Jones *et al*, 2003, 2004, 2007, 2012; Revell, 2007; Arnold *et al*, 2008; Pitchers *et al*, 2013), and experimental studies have revealed remarkable variations in **G** and **P** between closely related populations after inbreeding or induced bottlenecks (Phillips *et al*, 2001; Whitlock *et al*, 2002). Comparative studies of natural populations, usually involving few species, show variable levels of **G** or **P** matrix conservation (e.g. Steppan, 1997a; Arnold & Phillips, 1999; Arnold *et al*, 2008; Björklund *et al*, 2012). Larger-scale comparisons of mammal skulls using **P** matrices, on the other hand, suggest a largely conserved covariance structure (Marroig & Cheverud, 2001; Goswami, 2006a; Oliveira *et al*, 2009; Porto *et al*, 2009; Haber, 2015). Some of these studies (Marroig & Cheverud, 2001; Oliveira *et*

al, 2009; Porto *et al*, 2009) also found generally high and significant similarities when comparing phenotypic matrices of various mammals to **G** matrices estimated for particular taxa, further supporting a conserved genetic covariance structure in mammal skulls. Most larger-scale studies thus focus on the relatively high similarity of integration patterns between taxa, usually based on tests of the null-hypothesis of no similarity. On the other hand, Haber (2015) shows that, often, the same between-taxon comparisons also reject a null-hypothesis of no difference between **P** matrices. It is also relevant that morphological integration may be understood through two complimentary aspects: patterns (or matrix orientation, i.e. which elements are most correlated) and magnitude (or matrix shape, i.e. how intensely are elements correlated). The high similarity between **P** matrices found in comparative studies primarily reflects integration patterns, while magnitudes of integration, equally important in their evolutionary consequences (Pavlicev *et al*, 2009a, Marroig *et al*, 2009), were often found to be more variable (Marroig *et al*, 2001; Porto *et al*, 2009; Oliveira *et al*, 2009). Therefore, even though it is now relatively well-resolved that morphological integration does evolve, how much, which aspects, under which conditions and the phylogenetic scales at which it does are still very much open questions, as are the factors driving evolutionary changes in integration.

The reasons for conducting an in-depth study of the evolution of morphological integration in Feliformia are manifold. Previous works dealing with integration in other mammals provide a useful background against which to compare new results, allowing a comparison of the situation with that seen in other groups. Feliformia itself is also remarkably diverse in taxonomy (~130 extant species, in seven families), size (from the common dwarf mongoose, <300 g, to tigers weighing over >300 kg), morphology, diet (including insectivores, omnivores, frugivores and carnivores - Kissling *et al*, 2014, and having representatives of two hypercarnivore morphs, Cats and Hyaenas - van Valkenburgh, 2007) and other ecological aspects like social behaviour (Smith *et al*, 2012; Bailey *et al*, 2013; Noonan *et al*, 2015). Although the latter has never been explicitly tested as a factor contributing to morphological integration, the social brain hypothesis has posited that sociality may be related to brain size in mammals (Dunbar, 1998; Schultz & Dunbar, 2010; Smith *et al*, 2012; but see Finarelli & Flynn, 2009 and Holekamp *et al*, 2015). This suggests a possible effect of sociality on average skull morphology and/or in phenotypic integration, since brain growth is an important process affecting growth of the skull vault and base (Moore, 1981; Cheverud, 1995).

Noonan *et al* (2015) have also shown a relationship between sociality and burrowing classes (i.e. burrow use and amount of energetic investment in burrow excavation) in Carnivora, providing a further possible link between sociality and morphological integration. Moreover, relatively complete information is available for Feliformia regarding species' ecology (Smith *et al*, 2012; Kissling *et al*, 2014, among others) and also the group's phylogenetic relationships (e.g. Barycka, 2007; Patou *et al*, 2009; Nyakatura & Bininda-Emonds, 2012; Veron *et al*, 2015a,b; Li *et al*, 2016), providing an interesting opportunity to analyse changes in integration along the phylogeny and assess possible drivers of the evolution of integration. Finally, although morphological integration in Carnivora has been investigated previously, most existing studies focus on "evolutionary integration" (i.e. among-species covariances - Wroe & Milne, 2007; Goswami & Polly, 2010a; Goswami *et al*, 2011; Meloro & Slater, 2012), thwarting meaningful inferences on constraints or the evolution of integration. Those that do in fact focus on within-population integration deal with few species (Christiansen, 2008a; Goswami *et al*, 2014), or include a reduced number of Feliforms, especially non-felids (Goswami, 2006a - 12 feliforms, 5 of which felids; Goswami 2006b - 20 feliforms, 6 of which felids). In fact, Feliformia is underrepresented in most works dealing with morphological form and function in Carnivora (e.g. Mattern & McLennan, 2000; Slater & van Valkenburgh, 2009; Sicuro & Oliveira, 2011; Sakamoto & Ruta, 2012). While Felidae and Hyaenidae are usually present and often well-represented, the other families (Viverridae, Herpestidae, malagasy carnivores Eupleridae and monogeneric families Prionodontidae and Nandiniidae) are habitually absent or represented by few species.

One further interesting point in studying morphological integration within Feliformia is the clear difference in morphological disparity between its groups. Felidae in particular has large size differences among species, but a remarkably constant, easily-recognisable *cat-like* morphology (Martin, 1989; Van Valkenburgh, 2007), with shape variation usually explained mostly in terms of allometric relationships (Werdelin, 1983; Slater & Van Valkenburgh, 2009; Christiansen, 2008b; Sicuro, 2011; Sakamoto & Ruta, 2012). This size-constrained among-species variation might arise from selection pressure aligned with size, from a within-population variational constraint or possibly from both. It would be interesting, then, to compare the relative amount of within-population isometric size variation in felids and members of other families, to verify whether a variational constraint may be part of the reason for the mostly size-related diversification of cats. Comparing isometric size variation (i.e. size variation

independent of shape variation - Mosimann, 1970) to magnitudes of integration and related evolutionary metrics is also interesting, since previous studies have shown allometric size variation (represented by the first principal component of covariance matrices) to be a major factor contributing to integration in mammals (Porto *et al*, 2013), and consequently to how they may respond to selection (Marroig *et al*, 2009). Other families are not only much more variable in shape than felids, but also show eye-catching morphological convergences, like those found between Asian and African linsangs (*Prionodon* and *Poiana*, families Prionodontidae and Viverridae, respectively), between Asian and African palm civets (*Paradoxurus* and *Nandinia binotata*, families Viverridae and Nandiniidae, respectively) and between clades within the malagasy clade Eupleridae and others throughout Feliformia (*Cryptoprocta* and felids; subfamily Euplerinae and viverrids; subfamily Galidiinae and herpestids). This large number of convergent morphologies provides an interesting natural experiment to assess whether morphological integration tends to follow these convergences.

As mentioned above, previous large-scale analyses point to fairly stable integration patterns in Carnivora (Goswami, 2006a) and mammals in general, but variable integration magnitudes among mammals (Porto *et al*, 2009). Existing works also indicate a complex interplay between integration patterns and magnitudes, morphology (i.e. average phenotypic values), phylogenetic history and ecological aspects. The relatively stable integration patterns were often found to be unrelated to phylogenetic distances (Marroig & Cheverud, 2001; Christiansen, 2008a; Porto *et al*, 2009; Costa, 2013; Rossoni, 2013), but phylogenetic signal in integration has been detected in some groups (some Carnivora, Goswami, 2006a, including Feliformia; Catarrhini primates, Oliveira *et al*, 2009; Xenarthra, Hubbe, 2013; Ruminants, Haber, 2015). Conversely, the more variable magnitudes of integration relate to phylogenetic distance among mammalian orders (Porto *et al*, 2009; also within Xenarthra in Hubbe, 2013), but not within various less-inclusive groups (Catarrhini primates, Oliveira *et al*, 2009; Sigmodontinae rodents, Costa, 2013; phyllostomid bats, Rossoni, 2013). Patterns and magnitudes also change hand-in-hand in Catarrhini primates (Oliveira, 2009), but not in other groups (e.g. Hubbe, 2013; Costa, 2013; Rossoni, 2013), and average morphology correlates with integration patterns (Oliveira *et al*, 2009; Costa, 2013; Rossoni, 2013) and/or magnitudes (Costa, 2013) in some cases only.

Tests of ecological factors which might drive the evolution of integration included only diet so far, and have also had mixed results. Diet was identified as a

major feature influencing the evolution of integration patterns in new-world monkeys (Marroig & Cheverud, 2001, 2005), and may have influenced covariance matrix orientation among phyllostomids (Rossoni, 2013) and some Carnivoran clades (Caniformia, Arctoidea, Musteloidea, Mustelidae - Goswami, 2006a), whereas within Xenarthra (Hubbe, 2013), Carnivora as a whole and some of its subgroups (including Feliformia - Goswami, 2006a) diet was found to be unrelated to integration patterns. Contrastingly, diet influences on integration magnitudes have been found non-significant in the rare instances in which they have been tested (Hubbe, 2013; Rossoni, 2013).

In this work we use the largest dataset of feliform skulls to date to perform the most taxonomically-inclusive analysis of the evolution of morphological integration patterns and magnitudes within Feliformia so far. We characterise within-population integration patterns and magnitudes in **P** matrices at species or supra-specific levels (genus-level or lower), contrasting our results to *a priori* expectations of stability in integration patterns and greater variation in integration magnitudes, as found in previous studies of mammal skulls (e.g. Porto *et al*, 2009). For each **P** matrix, we also assess the relative proportion of total variation represented by isometric size, comparing the results among feliform clades and relating isometric variation to measures of integration magnitudes, as well as to evolutionary metrics previously shown to be highly dependent on integration magnitudes for most mammals (Marroig *et al*, 2009). Furthermore, we analyse relationships between patterns and magnitudes of integration, phylogeny, size, average skull morphology and two ecological factors which may bear on the evolution of both average morphology and integration (diet and social behaviour). Finally, we use a relatively under-explored method to decompose selection responses in character-specific response patterns (SRD - Marroig *et al*, 2011), allowing us to recognise which characters are more or less deviant in their covariance to other characters in the skull, which characters are responsible for the general structure of integration patterns revealed by usual **P** matrix comparisons, and also to identify the particular characters whose selection responses are most correlated to phylogeny and to two ecological factors (diet and sociality) possibly driving the evolution of morphological integration in Feliformia.

Materials and Methods

Choice of representation

Whereas many previous works on morphological integration make use of a set of interlandmark distances (e.g. Cheverud, 1995; Marroig & Cheverud, 2001, 2005, 2010; González-José *et al*, 2004; Porto *et al*, 2009, 2013; Oliveira, 2009; Haber, 2015), a variety of recent works started using geometric morphometrics (Rohlf & Marcus, 1993; Bookstein, 1996; Dryden & Mardia, 1998) to analyse morphological integration (e.g. Klingenberg & Zaklan, 2000; Goswami 2006a, b; Klingenberg, 2009; Goswami & Polly, 2010a,b; Goswami *et al*, 2014). As the variables used in geometric morphometrics correspond to 2- or 3-dimensional landmark coordinates after a Procrustes Superimposition procedure (Dryden & Mardia, 1998), morphological integration analyses using these methods must either use approaches based on a matrix of covariances between landmark coordinates (e.g. Klingenberg & Zaklan, 2000; Klingenberg, 2009) or use alternative methods to produce single between-landmark correlations (canonical correlations - Hotelling, 1936 or congruence coefficient - Burt, 1948, Abdi, 2007; see Goswami & Polly, 2010b). This entails at least two potential problems. First, as brought up by Rohlf & Slice (1990), Slice (1993), Walker (2000), Rohlf (2003), Adams *et al* (2004) and more recently by Linde & Houle (2009), as a result of its assumption of isotropic variation around each landmark, the Procrustes Superimposition procedure may impose a covariance structure on data, especially when actual variation deviates from isotropy, and consequently override the underlying biologically meaningful covariance structure. Secondly, the choice of the way to represent the covariance/correlation structure (landmark coordinate covariances, canonical correlations or congruence coefficients) is arbitrary and may lead to differing interpretations in some situations (Klingenberg, 2008; Klingenberg, 2009; Goswami & Polly, 2010b). The shape space underlying landmark covariances transformed into canonical correlations or congruence coefficients has also not been thoroughly studied, and is therefore not clearly understood. Also, Rohlf (2000a,b) has argued that methods based on complete trusses of interlandmark distances, with or without particular size-correction methods (e.g. Lele & Richtsmeier, 1991; Lele & Cole, 1996; Rao & Suryawanshi, 1996) may perform poorly in comparison to geometric morphometrics for detection of mean shape differences between groups, and may also possibly embed covariance patterns simply as a result of the mean shape of a structure

even if only random isometric variation is present, especially when the interlandmark distances involved have very different values (Rohlf, 2000b). These properties have been recognised specifically for configurations of few landmarks in two dimensions (mostly triangles, some analyses with 4-9 landmarks), when using complete trusses of interlandmark distances, and it is not clear that these difficulties would also apply to a selected set of interlandmark distances. One obvious aspect of interlandmark distances which may be seen as a problem for studies focusing on shape differences is their tendency to often show a predominance of size-related variation - leading past authors interpret the first principal component of distance-based morphometric data as overall size (e.g. Jolicœur & Mosimann, 1960). The usual dominance of size variation in sets of interlandmark distances arises not only because of the type of variable used, however, but also because measurements are usually chosen to represent biologically relevant characters, and overall size is in fact a relevant source of biological variation. Particularly, while this prevalence of size variation may obviously pose difficulties and/or require additional steps to analyse shape differences, it represents an important factor for morphological integration (Marroig & Cheverud, 2001, 2010; Porto *et al*, 2013), so using methods that remove size variation *a priori* may not be appropriate for studies of integration. Also, methods to separate size and shape variation in distance-based morphometrics do exist for when it may be desirable to do so (e.g. Mosimann, 1970; Somers, 1986, 1989; see below). For the reasons mentioned, we favoured the use of distance-based methods for the morphological integration analyses performed here, employing the same set of interlandmark distances used in Porto *et al* (2009, 2013) to allow direct comparison with results from other mammalian clades. The measurements chosen for this study, specifically, were chosen so as to reflect specific dimensions of skull bones and structures, enabling local understanding of ontogenetic, genetic and functional processes (Cheverud, 1995; Marroig & Cheverud, 2001) and also allowing meaningful interpretation of single traits - unlike landmark coordinate data from geometric morphometrics analyses, which only acquire meaning in relation to the whole set of procrustes superimposed landmark coordinates.

Sample and Variables

A total of 2740 skulls were measured for this study, representing 124 feliform taxa. The material examined is deposited in the following institutions: Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo), Museu Nacional da

Universidade Federal do Rio de Janeiro (MNRJ, Rio de Janeiro), American Museum of Natural History (AMNH, New York), Museum für Naturkunde (ZMB_Mam, Berlin), Naturhistorisches Museum Wien (NMW, Vienna), Muséum National d'Histoire Naturelle (MNHN, Paris), Zoologisches Forschungsmuseum Alexander Koenig (ZFMK, Bonn), Přírodovědecké muzeum - Národní muzeum (NMP, Prague), University Museum of Zoology, Cambridge (UMZC, Cambridge - UK), Senckenberg Naturmuseum Frankfurt (SMF, Frankfurt am Main) and Naturalis Biodiversity Centre (Naturalis, Leiden). All digitised skulls were adults or young adults (recognised based on completely erupted dentition and the suture closure levels), and preference was given to specimens including information on sex and collection locality.

Three-dimensional coordinates were recorded for 20 landmarks on each specimen (8 on the sagittal line and 12 on both sides of the skull; **Figure 2-1A**) using a Microscribe MX digitizer. All procedures after data acquisition were performed in the R programming environment (R Core Team, 2015).

Data processing included unification of landmarks digitised with the skull in different positions (as not all landmarks could be digitised with the skull fixed in a single position), followed by reflection and superimposition of symmetrical landmarks on each skull, masking fluctuating asymmetry but allowing the use of data from specimens missing landmarks on one side. In order to identify digitisation errors and outliers, we performed a Procrustes superimposition of each taxon's symmetrical configurations, analysed the distribution of Procrustes distances (using the "plotOutliers" function from the R package "geomorph") and compared discrepant skulls to photographs taken during data collection. This led to exclusion of 20 possible errors and outliers from the database. All further analyses used as characters the 35 linear distances used in previous works on morphological integration in mammals (Porto *et al*, 2009, 2013 - **Figure 2-1B**), calculated from the symmetrical configurations of 20 landmarks. The complete list of digitised skulls is available in **Appendices 1 and 2**; the latter lists outliers removed from analyses). A more detailed description of data collection and processing procedures is provided in **Appendix 3**.

Figure 2-1. Landmarks (A) and representation of the linear measurements (B) used as characters in this study. The list of 35 linear measurements used follows Porto *et al* (2009) and includes: IS-PM; IS-NLE; IS-PNS; PM-ZS; PM-ZI; PM-MT; NLE-NON; NLE-ZS; NLE-ZI; NON-BR; NON-PNS; BR-PT; BR-APET; PT-APET; PT-BA; PT-EAM; PT-ZYGI; PT-TSP; ZS-ZI; ZI-MT; ZI-ZYGI; ZI-TSP; MT-PNS; PNS-APET; APET-BA; APET-TS; BA-EAM; EAM-ZYGI; ZYGI-TSP; LD-AS; BR-LD; OPI-LD; PT-AS; JP-AS; BA-OPI.

Most specimens (2123 skulls) were digitised twice, allowing estimation of linear distance repeatability to account for measurement errors (Lessels & Boag, 1987). Repeatability calculated separately for each species and character had average values over 0.93 in all cases; low values were found for BA-OPI in *Arctogalidia trivirgata* (0.52) and for APET-TS in *Crossarchus obscurus* (0.77), both species having relatively low numbers of specimens with replicated measurements (10 and 15 for *A. trivirgata* and *C. obscurus*, respectively). BA-OPI and APET-TS include landmarks whose digitisation met some difficulties in some specimens. However, repeatability values for these measurements was high in all other taxa, and also when analysing pooled supra-specific data for the genera *Crossarchus* and *Arctogalidia* (minimum repeatability ~0.89 for both). The lower repeatability values in these two cases, therefore, probably reflect

relatively low inter-specimen variance for these measurements in the sampled specimens. More detailed results of character repeatability may be found in **Appendix 4**. As the greatest majority of repeatability values obtained was high, measurement error was considered to have negligible impacts on the results. Therefore, all subsequent analyses used the average replicated measurements for skulls which had them. Deviation from normality (Lilliefors tests, $\alpha < 0.05$) in the residuals of linear measurements after outlier analyses and correction for external sources of variation (see below) were found for ≤ 4 characters in most taxa, up to a maximum of 7 characters in *Neofelis nebulosa*. Impacts of deviations from normality on our results are thus expected to be minimal.

We initially used 2605 skulls for estimation of covariance matrices representing 63 species with sample sizes ≥ 7 from all 7 currently recognised feliform families. Matrix estimation even for species with very low sample sizes (7 to 16) was performed tentatively, in order represent rare species with few samples available in collections. However, since interpretation of covariance matrices estimated with low sample sizes is conjectural at best, most analyses were performed using a set of 53 better-estimated matrices (using a total of 2553 skulls), including species-level matrices as well as supra-specific matrices, generated for less well-represented clades by grouping sister taxa. Fifty one (51) other skulls representing 14 species with sample sizes between 3 and 6 were also included for estimation of a pooled within-group covariance matrix for Feliformia (**W** - see below).

Taxonomy

We used Wozencraft (2005)'s taxonomy as a basis for this work, but include various changes proposed in recent results in carnivore taxonomy and systematics. The complete list of the taxonomic decisions taken for this work is found in **Appendix 3** (***Taxonomy, species confirmation and reidentification*** section).

Covariance matrix estimation and comparison of Integration Patterns

We initially estimated phenotypic covariance matrices (**P**) for 63 species with sample sizes ≥ 7 , in order to perform a tentative analysis of species-specific results including some rare species for which few samples were available in visited collections (e.g. *Galidictis fasciata*, *Poiana richardsoni*). As mentioned above, interpretation of covariance matrices estimated with low sample sizes is conjectural at best. Therefore, in order to allow more reliable analyses, we generated better-estimated supra-specific

covariance matrices for less well-represented clades by grouping sister taxa. We thus obtained better-estimated matrices for a set of 53 taxa, most with sample sizes ≥ 35 . Five taxa, corresponding to rarer taxa with limited samples available in museums, were represented in the set of 53 better-estimated matrices by matrices estimated with sample sizes <35 , but ≥ 17 : *Hemigalus derbyanus* (Viverridae), the genus *Prionodon* (Prionodontidae), *Salanoia concolor*, *Eupleres goudotii* and *Fossa fossana* (Eupleridae). Sampling effects on these smaller samples means the results for these matrices must be interpreted with greater care, but their inclusion was deemed relevant to allow representation of all feliform subfamilies in the analyses.

Prior to matrix estimation, we identified significant external sources of variation not relevant for this study (age, sex, subspecies, historical time, plus species for supra-specific matrices, as well as their interactions) using multivariate analyses of variance (MANOVAs) using the Wilk's lambda statistic, univariate ANOVAs and analysis of effect sizes. For sex and subspecies, after initial assignment based on museum labels, unclassified specimens and those with conflicting information were reclassified using Principal Component Analysis (PCA) and discriminant analysis (LDA), allowing identification and correction for these sources of variation for all taxa (see **Appendix 5** for a more detailed description of the methods for identification of external sources of variation and matrix estimation). The effects of significant external sources of variation were removed using multivariate linear models adjusted for each clade; phenotypic covariance matrices were then estimated using linear models residuals, thus representing "within-population" phenotypic integration. **Table 2-1** shows sample sizes and external sources of variation removed for each species or supra-specific clade.

Table 2-1. List of Feliform taxa for which covariance matrices were estimated, sample size (n), number of specimens measured twice (reps) and sources of variation corrected for each taxon. Sources of variation are age, sex, subspecies (ssp), species/subspecies (sp/ssp), captivity (cat) and historical time (hist). * denotes interaction between factors. ^a indicates taxa not included in the set of 53 better-estimated matrices.

Family	Species	n	Model	Family	Species	N	model
Eupleridae	<i>Cryptoprocta ferox</i> ^a	34	age+sex*cat	Herpestidae	<i>Atilax paludinosus</i>	50	sex+ssp
	<i>Eupleres goudotii</i>	18	-		<i>Crossarchus obscurus</i> ^a	31	-
	<i>Fossa fossana</i>	25	Sex		<i>Crossarchus platycephalus</i> ^a	39	age+capt
	<i>Galidia elegans</i>	46	sex+age+ssp		<i>Cynictis penicillata</i>	51	ssp*cat
	<i>Galidictis fasciata</i> ^a	11	-		<i>Galerella sanguinea central</i> ^a	36	ssp
	<i>Salanoia concolor</i>	17	Age		<i>Galerella sanguinea south</i> ^a	14	sex+age
	<i>Cryptoprocta (Genus)</i>	36	sex+sp/ssp+age		<i>Helogale parvula</i>	50	ssp+age+cat
Felidae	<i>Acinonyx jubatus</i>	48	sex+ssp+age		<i>Mungos mungo</i>	62	ssp+age
	<i>Caracal caracal</i>	50	sex+age		<i>Suricata suricatta</i>	49	age+cat
	<i>Catopuma temminckii</i>	40	sex+age		<i>Urva javanica</i>	50	sex+ssp
	<i>Felis catus</i>	52	age*hist+sex		<i>Urva urva</i>	44	age+sex+ssp
	<i>Felis margarita</i>	49	age+sex*cat		<i>Crossarchus (Genus)</i>	74	sp/ssp*cat+age
	<i>Felis silvestris</i>	63	age+ssp+sex*cat		<i>Galerella sanguinea group</i>	51	sp/ssp+age
	<i>Leopardus colocolo</i> ^a	11	Sex	Hyaenidae	<i>Crocuta crocuta</i>	50	sex*ssp+age
	<i>Leopardus geoffroyi</i>	47	sex+ssp+cat		<i>Hyaena hyaena</i>	51	age+cat+ssp
	<i>Leopardus guttulus</i> ^a	43	Sex		<i>Parahyaena brunnea</i>	48	age+ssp+sex
	<i>Leopardus mitis</i>	72	sex+ssp+age		<i>Proteles cristata</i>	44	ssp+age
	<i>Leopardus tigrinus</i> ^a	8	Age	Nandiniidae	<i>Nandinia binotata</i>	49	sex+age+ssp
	<i>Leopardus wiedii</i>	50	sex+ssp	Prionodontidae	<i>Prionodon linsang</i> ^a	13	ssp+age
	<i>Leptailurus serval</i>	51	sex*ssp+age+cat		<i>Prionodon pardicolor</i> ^a	7	ssp
	<i>Lynx lynx</i>	50	ssp+age		<i>Prionodon (Genus)</i>	20	sp/ssp
	<i>Lynx rufus</i>	46	ssp+age+sex	Viverridae	<i>Arctictis binturong</i>	50	ssp+age
	<i>Neofelis diardi</i> ^a	40	sex+age+cat		<i>Arctogalidia stigmatica</i> ^a	31	sex
	<i>Neofelis nebulosa</i> ^a	17	sex+age+ssp		<i>Arctogalidia trivirgata</i> ^a	18	-
	<i>Panthera leo</i>	49	sex+ssp+cat		<i>Civettictis civetta</i>	51	sex*ssp
	<i>Panthera onca</i>	54	age+ssp+sex		<i>Genetta genetta</i>	57	ssp*sex
	<i>Panthera pardus</i>	52	sex+ssp+age		<i>Genetta maculata</i>	59	ssp+sex+cat+age
	<i>Panthera tigris</i>	47	sex+age+ssp+cat		<i>Genetta servalina</i>	44	ssp
	<i>Panthera uncia</i>	46	sex+ssp+age		<i>Hemigalus derbyanus</i>	33	ssp+sex+age
	<i>Prionailurus bengalensis</i>	50	Ssp		<i>Paguma larvata</i>	50	ssp+cat
	<i>Prionailurus viverrinus</i> ^a	12	cat+ssp		<i>Paradoxurus musanga</i>	49	ssp+age
	<i>Puma concolor</i>	50	ssp+age+sex		<i>Poiana richardsonii</i>	8	-
	<i>Puma yagouaroundi</i>	47	ssp+sex		<i>Viverra zibetha</i>	47	ssp+age
	<i>Leopardus tigrinus group</i>	53	sp/ssp+sex		<i>Viverricula indica</i>	55	ssp+age+sex
	<i>Neofelis (Genus)</i>	57	sp/ssp+sex+age+cat		<i>Arctogalidia (Genus)</i>	49	sp/ssp+sex+cat

To compare morphological integration patterns, we calculated pairwise similarity between covariance matrices (**P**) using the Random Skewers (RS) method (Cheverud 1996a; Cheverud & Marroig, 2007). This metric is based on Lande (1979)'s equation of multivariate response to selection ($\Delta z = \mathbf{G}\beta$). For each pair of taxa, their phenotypic covariance matrices (**P**, as a surrogate for **G**) were multiplied by a large number (1000 here) of random selection vectors (β) extracted from a normal distribution and normalised to a length of one (Cheverud & Marroig, 2007), producing pairs of selection response vectors (Δz). The Random Skewers similarity metric for each pair of matrices is the mean of the vector correlations of Δz pairs produced as a response to each random β . Pairwise similarities were organised in two taxon-by-taxon Integration Pattern Similarity Matrices (IPSM): one for the set of 63 species-level **P** matrices and one for the 53 taxa with better-estimated matrices ($n \geq 17$).

We used two methods to assess the reliability of estimated matrices. First, we calculated matrix repeatability (t) for each matrix using 100 Bootstrap resamples of linear model residuals for each taxon with the same sample size as the original data, comparing each resample to the original matrix using the RS method (Marroig & Cheverud, 2001). The average similarity between resamples and the original matrix is used as the repeatability for each taxon. Repeatability values were also used to adjust RS similarity values to account for sampling errors (Cheverud, 1996), according to the formula: $RS_{ABadj} = RS_{ABobs} / (t_A \cdot t_B)^{1/2}$, where RS_{ABobs} is the observed (calculated) similarity between matrices, t_A and t_B are the repeatability values for matrices **A** and **B**. We focus our discussion only on adjusted similarity values, and use these for all further analyses. Additionally, we performed a rarefaction analysis starting from a pooled within-group matrix joining *Felis silvestris* and *Felis catus*. Although treated as distinct here, *F. catus* and *F. silvestris* are often considered conspecific (e.g. Driscoll *et al*, 2007), thus use of this pooled matrix allows this analysis to start from a large sample (116 specimens) while still retaining biological significance. The linear model used for estimating the *F. silvestris* + *F. catus* matrix included age and sex*captivity (both factors and its interaction), in addition to species/subspecies. The rarefaction analysis consists in stepwise Jackknife resampling of linear model residuals from the full sample, from $n=115$ to $n=3$ individuals, with 10 resamples taken for each step. Covariance matrices were calculated for each rarefied dataset and compared to the original *Felis silvestris* + *catus* matrix, generating a distribution of self-similarity values for different sample sizes, which we compared with the distributions of pairwise

similarities for the 63 species-level original matrices at different taxonomic levels (between families, within families and within genera). The covariance matrix for *Felis silvestris* + *catus* shows a concentration of a relatively high amount of variation in the first Principal Component, which may lead to a smaller decrease in similarity values with decreasing sample sizes in the rarefaction analysis. To assess this possibility, we performed additional rarefaction analyses for 3 taxa from other families with lower total sample sizes, but also less variation explained by the first Principal Component (*Hyaena hyaena*, Hyaenidae, n = 51; *Civettictis civetta*, Viverridae, n = 51; *Crossarchus* genus, Herpestidae, n = 74). The results of these additional rarefaction analyses is shown in **Appendix 6**.

An alternative method using rarefaction results to adjust RS similarity values based on a regression of similarity values on the inverse of the harmonic mean of the matrices compared (Steppan, 1997b) was also tested, using rarefactions of the *Felis silvestris* + *F. catus* matrix and also of the *Leopardus mitis* matrix. These procedures produced similar results to those using the adjustment mentioned above. The results of RS similarity adjusted by this alternative method are shown in **Appendix 7**.

In order to visualise the structuring of morphological integration patterns among taxa, integration pattern similarities were converted to a dissimilarity matrix (1-IPSM) and decomposed using Principal Coordinate Analysis (PCoA - Gower, 1966). PCoA produces "trait" axes with decreasing amounts of variation (as in PCA), organising them so that euclidean distances between individuals approximate the original dissimilarity matrix. The set of axes with non-negative associated eigenvalues may be treated as an "integration space" in which species are scored based on the similarity of their integration patterns. For visualisation purposes, we used the two first PCO axes to represent the organisation of taxa in the integration space for the 63 species-level matrices and for the 53 better-estimated matrices. Summed, the two first PCO axes explain 34.21% and 39.03% of the total variation in integration patterns for the 63 species-level matrices and the 53 better-estimated matrices, respectively. A broken-stick-model (Frontier, 1976) indicates that the first 7 and 5 PCO axes include relevant information for the integration patterns of the 63 species-level and 53 better-estimated matrices, respectively (**Appendix 8**). **Appendix 8** also shows the plots for the third and fourth PCO axes of both sets of matrices. While the plot of the first two PCO axes shown in the results do not explain the greatest part of the variance in integration patterns, they do show structuration in relevant axes of variation existing in the data,

and may help understand which groups of taxa differ the most in their integration patterns. It should be stressed that all quantitative analyses used the complete variation existing in matrix similarity patterns, and not just the first PCO axes..

We also performed **P** matrix pairwise comparisons using the Krzanowski Correlation (Krz) method (Krzanowski, 1979; Marroig *et al*, 2010) based on a subspace of the first 16 Principal Components (PCs) of each matrix. Although some results differed from those for the RS method, we focus our discussion and perform all further analyses using RS values only, given that this is the only metric directly based on evolutionary theory (Hansen & Houle, 2008). Results with the Krz method for the 63 species-level ($n \geq 7$) and the 53 better-estimated ($n \geq 17$) matrices are shown in **Appendix 9**.

Although comparisons of integration patterns for the 63 species-level matrices allow some interpretation, we decided to restrict all further analyses to the 53 better-estimated matrices to reduce possible effects of sampling errors in our results.

To verify whether covariance matrices for each sex had similar orientation and shape (even if centred on different mean character values), we estimated sex-specific **P** matrices for the 53 better-estimated taxa and used the RS method to compare, within each species, matrices for males and females to each other and to the original matrix using all specimens. We found a mean similarity of 0.901 for comparisons between sex-specific and complete matrices, and 0.778 for comparisons between male and female matrices. As the sample size for sex-specific matrices was much smaller, similarities between them are expected to be lower. Given this bias, we consider that matrices for both sexes tend to be similar enough to allow interpretation of pooled matrices. Results for comparison of sex-specific matrices can be seen in **Appendix 10**.

Integration Magnitudes and Evolutionary Metrics

We represent the overall magnitude of integration for the **P** matrices of the 53 better-estimated taxa with two commonly-used indexes: the mean coefficient of determination (r^2 - Van Valen, 1974) and the coefficient of variation of eigenvalues (ICV- Shirai & Marroig, 2010). For calculation of r^2 values, **P** matrices were converted to correlation matrices using the R function `cov2cor`; ICV values were calculated directly from covariance matrices.

Marroig *et al* (2009) have defined two metrics which represent different aspects of a population's evolutionary capabilities: average flexibility ($\bar{f}$) and constraints.

Average flexibility $\bar{f}$ is defined as the average vector correlation between a large number of random selection gradients (β) applied to a covariance matrix $\mathbf{P}$ (or $\mathbf{G}$) and their respective evolutionary responses (Δz). As such, $\bar{f}$ represents a measurement of a population's ability to generate responses to selection aligned to the actual direction of selection. As defined in Marroig *et al* (2009), constraints correspond to the average vector correlation between evolutionary responses Δz to a large number of random β applied to a covariance matrix ($\mathbf{G}$ or $\mathbf{P}$) and the first principal component of the matrix in question. Higher magnitudes of integration may either accelerate or constrain evolutionary responses in particular instances of selection, depending on whether selection is aligned to a population's main multivariate directions of greatest variance (Schluter, 1996; Arnold *et al*, 2001; Marroig *et al*, 2010). Marroig *et al* (2009) have shown, however, that integration magnitudes consistently show high negative correlation to average flexibility ($\bar{f}$), and high positive correlation to constraints for skulls of various mammalian orders.

Here we correlated Integration Magnitude indexes (r^2 and ICV) and Marroig *et al* (2009)'s evolutionary metrics ($\bar{f}$ and constraints) among themselves, as well as to the proportion of variation represented by the first principal component of each $\mathbf{P}$ matrix (% PC1), in order to test whether the relationships between these variables verified by Marroig *et al* (2009) for representatives of diverse mammal orders are maintained for a dataset focused on a single suborder. We also correlated these metrics of integration magnitude, size variation and evolutionary aspects to the proportion of within-population isometric variance (see below).

In order to compare integration magnitudes between Feliform taxa, we also generated a distribution of 200 r^2 values for each taxon using MonteCarlo parametric resamples based on linear model residuals and the original covariance matrix for each taxon. We additionally compared r^2 values for Feliforms with those previously published for other mammals (Porto *et al*, 2009).

Since five of the 53 better-estimated matrices still have relatively low sample sizes (< 35), we conducted some analyses to assess the influence of sample size on r^2 estimates. Regressions of r^2 values on sample size were nonsignificant, whereas the standard deviation of bootstrapped r^2 values does possibly show a dependence on sample size, although this effect does not seem too strong (**Appendix 11**). This suggests that lower sample sizes may lead to less accurate estimations of r^2 , but do not produce a

systematic bias on estimated values. The same logic probably applies to other metrics of integration magnitudes, related evolutionary aspects and %PC1, as well as for the proportion of isometric variation, described below.

Isometric Variation

We explicitly calculated the proportion of within-population isometric variation (%iso) for each of the 53 better-estimated taxa to directly assess whether there are differences in the relative contribution of isometric size variation to total skull variation between Feliform families, particularly between felids and other families, as well as to verify how %iso relates to other measures of size variation, to integration magnitudes and to related evolutionary metrics. To do so, we used a procedure equivalent to the method of PCA on "double-centred" log-transformed data (Somers, 1989; Claude *et al*, 2007), in which the mean of each row ("individuals") are subtracted from each cell of the data matrix as well as subtracting the means per column ("variables") as in ordinary PCA. To perform this procedure, we generated logarithmic character values of 34 linear measurements (excluding PT-TSP) for the 53 better-estimated taxa and corrected them for the same external sources of variation used when estimating the original **P** matrices; the residuals were used to build **log P** matrices (in logarithmic scale). PT-TSP showed extreme intra-specific variations in some species (see **Appendix 3**), leading to a large contribution of this measurement in total variation in the logarithmic scale. Therefore, variation in PT-TSP may not be solely affected by growth through multiplicative processes, and it might not be appropriate to represent this distance in a logarithmic scale (Houle *et al*, 2011), which led to the decision to remove this measurement for estimation of the **log P** matrices.

After the step above, we centralised log-scale linear model residuals for each taxon on character averages to recover a matrix of "model-corrected log-scale character values", instead of residuals centred on 0. After that, for each specimen, we subtracted from each character the arithmetic mean of the 34 character values (equivalent to the logarithm of the geometric mean (gm) of the 34 character values in the natural scale). This procedure produced a dataset free from the influence of a standardised isometric size variable (i.e. the geometric mean of measurements). This procedure may be represented in matrix form as:

$$\log A - \log GM = \log A_{sf}$$

or, in expanded form:

$$\begin{aligned} & \begin{pmatrix} \log(a_{11}) & \dots & \log(a_{1k}) \\ \dots & \dots & \dots \\ \log(a_{n1}) & \dots & \log(a_{nk}) \end{pmatrix} - \begin{pmatrix} \log(gm_1) & \dots & \log(gm_1) \\ \dots & \dots & \dots \\ \log(gm_n) & \dots & \log(gm_n) \end{pmatrix} \\ &= \begin{pmatrix} \log(a_{11}) - \log(gm_1) & \dots & \log(a_{1k}) - \log(gm_1) \\ \dots & \dots & \dots \\ \log(a_{n1}) - \log(gm_n) & \dots & \log(a_{nk}) - \log(gm_n) \end{pmatrix} \end{aligned}$$

where a_{nk} is the value of character k for the n -th individual (after correction for fixed factors), gm_n is the geometric mean of the k characters for the n individual, $(\prod_{i=1}^k x_i)^{\frac{1}{k}}$ and $\mathbf{A}_{sf}$ is the matrix of size-corrected data.

As arithmetic means in the log scale correspond to the logarithm of the geometric means in the natural scale, this method (and therefore the double-centring of Somers, 1989) is the log-scale equivalent of Mosimann (1970)'s procedure for producing shape variables dividing each character by a "standard size variable", using the geometric mean as the chosen size variable.

Estimation of covariance matrices using this new size-corrected dataset produces size-free residual phenotypic shape covariance matrices $\log \mathbf{P}_{sf}$. A principal component analysis on a $\log \mathbf{P}_{sf}$ matrix estimated with sample size ≥ 34 produces eigenvectors uncorrelated to the theoretical isometric size vector for 34 characters with elements $1/\sqrt{k}$ (Jolicoeur, 1963), except for the last eigenvector, which is perfectly correlated to the theoretical isometric vector and has an associated eigenvalue of 0, indicating the absence of isometric size variation (Somers, 1989; Claude *et al*, 2007). Matrices with sample size < 34 produce a number of size-uncorrelated vectors equal to their sample size - 1, while the remaining eigenvectors have variable correlations to the isometric vector.

The use of the log-scale for the procedure above keeps an additive relationship between variances in size and shape. Therefore, total variance for each $\log \mathbf{P}$ matrix equals the sum of the total variance of its respective residual shape matrix $\log \mathbf{P}_{sf}$ and the total variance in the "isometric size matrix" $\log \mathbf{GM}$ described above. The total variation in the $\log \mathbf{P}$ and $\log \mathbf{P}_{sf}$ matrices may be represented by the trace (sum of the diagonal) of these matrices. The total variation in $\log \mathbf{GM}$, likewise, may be represented by the trace of its diagonal covariance matrix $\text{cov}(\log \mathbf{GM})$. That is:

$$\text{tr}(\log \mathbf{P}) = \text{tr}(\text{cov}(\log \mathbf{GM})) + \text{tr}(\log \mathbf{P}_{sf})$$

As $\text{cov}(\mathbf{\log GM})$ is a diagonal matrix, having the variance of $\log gm$ ($s_{\log gm}$) on all k diagonal cells, the total variation in $\mathbf{\log GM}$ may be represented simply as:

$$\text{var}(\mathbf{\log GM}) = k \cdot s_{\log gm}$$

Therefore, the relationship between total, size and shape variances may be represented as

$$\text{tr}(\mathbf{\log P}) = k \cdot s_{\log gm} + \text{tr}(\mathbf{\log P}_{sf})$$

where k is the number of characters (34 in this case) and $s_{\log gm}$ is the variance of the geometric mean of character values between individuals for the taxon in question. The proportion of isometric variation (%iso) may thus be calculated directly as the rate between isometric size variation and total variation:

$$\frac{k \cdot s_{\log gm}}{\text{tr}(\mathbf{\log P})}$$

As an alternative way to extract isometric size, we scaled the landmark configuration of each specimen analysed to unit centroid size (CS), extracting linear distances from the scaled configurations, then multiplying all resulting distances by the average centroid size of each taxon. A Principal Component Analysis of $\mathbf{P}$ matrices produced from log-transformed linear distances extracted in this manner had all eigenvectors still correlated to the theoretical isometric vectors. For this reason we preferred the use of the approach described above.

Proportions of isometric variation for each taxon were correlated to %PC1, to verify how closely the variation in the first principal component relates to isometric size variation. In order to assess how much isometric variation itself contributes to integration magnitudes and related properties with evolutionary significance, the proportions of isometric variation were also correlated to integration magnitude indexes (r^2 , ICV) and the evolutionary metrics mentioned in the previous section ($\bar{f}$, constraints). Additionally, in order to compare the proportion of isometric variation between taxa, we generated a distribution of 100 %iso values based on Bootstrap resamples of character average-centralised log-scale linear model residuals.

As an additional way to assess the importance of isometric variation for each species, we also calculated the correlation between character coefficients on the first principal component (PC1) of each **log-scale** $\mathbf{P}$ matrix and the theoretical log-scale isometric vector for 34 characters.

Integration, size, phylogenetic, morphological and ecological distances - Comparative Methods

To test relationships between morphological integration, morphology and ecology, as well as relations between these aspects and the phylogeny (i.e. phylogenetic signal), we built taxon-by-taxon matrices for the 53 better-sampled taxa representing phylogenetic and morphological distances, as well as distances in two aspects of ecology: diet and social behaviour.

The phylogenetic distance matrix (PDM) was built based on the most recent species-level phylogeny including all of Feliformia (Nyakatura & Bininda-Emonds, 2012), including some alterations to reflect the taxonomy used for this work and the results of recent works on the taxonomy and systematics of feliformian families (Wilting *et al*, 2007; Christiansen, 2008c; Patou *et al*, 2009; Nascimento, 2010; Ruiz-Garcia *et al*, 2012; Trigo *et al*, 2013; Li *et al*, 2016; Veron *et al*, 2015a,b, Veron *et al*, 2014; Rapson *et al*, 2012). An in-depth description of the alterations done and the phylogeny used can be found in **Appendix 12**. The phylogenetic distance matrix was obtained using the function "cophenetic.phylo" from the R package "ape" on the phylogeny, including branch lengths.

A morphological distance matrix (MDM) was produced by calculating pairwise Mahalanobis distances between taxa using the function "MultiMahalanobis" from the R package "evolq" (Melo *et al*, 2015) and a pooled within-group covariance matrix for Feliformia (**W**), estimated accounting for external sources of variation (including species) as mentioned above. **Appendix 8** provides a representation of the morphospace represented by the 2 first axes of a PCO on Mahalanobis distances, which explains 72.78% of the total variation in mean morphology. A broken-stick-model shows that the 3 first PCO axes have relevant information regarding the mean morphology; this analysis and a plot of the second and third PCO axes for Mahalanobis Distances are also shown in **Appendix 8**.

Ecological distance matrices for diet (DDM) and sociality (SDM) were created using range-normalised Manhattan Distance (i.e. the distance used for quantitative traits in Gower, 1971) averaged over all dietary items or all types of social behaviour included in the Feliformia diet and sociality databases described below. The Feliform diet database used data from Kissling *et al* (2014)'s mammalian diet database for the 13 dietary items consumed by at least one Feliform species. Information was added for species absent from the original database by using data from closely related species, and

for superspecific taxa by using data from one species belonging to the group: *Leopardus mitis* (as *L. pardalis*); *Paradoxurus musanga* (as *P. hermaphroditus*); *Galerella sanguinea* group (as *G. sanguinea*); *Leopardus tigrinus* group (as *L. tigrinus*); *Neofelis* (Genus - both *Neofelis* share the same diet); *Crossarchus* (Genus - all *Crossarchus* included here share the same diet); *Arctogalidia* (Genus - as *A. trivirgata*); *Prionodon* (Genus - as *P. linsang*). For the sociality database, we used Smith *et al* (2012)'s five social behaviour categories (group hunting, intergroup coalition formation for territory defence, intragroup coalition formation, cooperative protection from predators, and alloparenting), the first four classified as present (1) or absent (0), while alloparenting is classified as present (1), partially present (0.5 - defined as sharing of a communal den without true alloparental care), or absent (0). We obtained sociality data for Feliform taxa both from Smith *et al* (2012)'s database and additional sources (Goldman, 1987; Taylor & Meester, 1993; Macdonald *et al*, 2000; Gilchist *et al*, 2009; Bailey *et al*, 2013; Kingdom & Hoffman, 2013; IUCN, 2013; ADW: <http://animaldiversity.org>; EOL: <http://eol.org>). Data for species present in Smith *et al* (2012)'s database were sometimes changed when they contrasted with information from other sources. Sociality data could not be found for three of the 53 better-estimated taxa: *Arctogalidia* (Genus), *Genetta servalina* and *Salanoia concolor*; these taxa were removed from all analyses including sociality. **Appendix 8** shows representations of the resulting ecological spaces for diet and sociality built using the 2 first axes of Principal Coordinate Analyses on DDM and SDM, respectively.. The two first PCO axes explain 63.54% and 93.24% of the total variation for diet and sociality, respectively. Broken-Stick-Models indicate that relevant information for diet and sociality are present in the first 4 and 2 PCO axes, respectively (**Appendix 8**). A representation of the third and fourth axes of dietary variation is also shown in **Appendix 8**. Interpretation of the ecological space for diet indicates the first principal coordinate (PCO1 - 36.51% of total variation) mainly distinguishing carnivores from herbivores/ invertivores, and PCO2 (27.03%) related to "diet breadth" (defined here as the sum of values in different food categories, thus related to the variety of food items consumed). The ecological space for social behaviour shows PCO1 (76.34% of total variation) related to the "degree of sociality" (i.e. number of social behaviours shown), while PCO2 (16.90%) mostly distinguishes "group hunters" (e.g. *Crocota crocuta*, *Panthera leo*, other felids, *Cryptoprocta*) from species displaying collaborative defence and alloparenting (e.g. many social herpestids, *Parahyaena brunnea*). The complete diet and sociality databases are available in **Appendix 13**, and

a more in-depth description of the methods used for obtaining diet and sociality distance matrices is available in **Appendix 14**. A short discussion of alternative methods considered for calculating dietary distance and a statement of the reasons for choosing the method described above is presented in **Appendix 15**.

Matrix Correlations followed by Mantel Tests were used to assess the relationships between Integration Patterns (1-IPSM) and Magnitude (r^2 values converted to pairwise distances, i.e. difference between the values for each pair of taxa), body size (log gm; taxon average of the natural logarithm of the geometric mean of the 35 linear measurements for each specimen, converted to pairwise distances as described above for r^2), average morphology (MDM), diet (DDM), sociality (SDM) and phylogeny (PDM) for the better-estimated taxa. Analyses were done for Feliformia as a whole and also for various phylogenetic groupings (with $n \geq 5$ taxa) within the suborder (Feloidea = families Felidae + Prionodontidae; Viverroidea = families Viverridae + Hyaenidae + Herpestidae + Eupleridae; family Felidae; subfamily Felinae; subfamily Pantherinae; family Viverridae; HyHeEu = families Hyaenidae + Herpestidae + Eupleridae; HeEu = families Herpestidae + Eupleridae; family Herpestidae; family Eupleridae). Most of these comparisons excluded the three taxa for which sociality information could not be found (see above). Conversely, sociality (SDM) was not included in the comparisons for Viverridae (which showed no social behaviour for any species) and Eupleridae (which would retain only 4 species if excluding *Salanoia concolor*, for which no information on sociality was found). As we use 1-IPSM for Integration Patterns, all factors (integration patterns, magnitudes, phylogeny, average morphology, diet and sociality) were represented by distance/dissimilarity matrices. Therefore, positive correlations are expected whenever a significant relationship exists between factors. We performed partial Mantel tests using Phylogenetic Permutations (Lapointe & Garland, 2001; Harmon & Glor, 2010) whenever two factors were found to have significant correlations and at least one of them was also significantly correlated to phylogeny (i.e. showed significant phylogenetic signal), in order to assess the correlation between characters after correcting for phylogenetic relatedness. Mantel tests were performed using the R function MantelCor ("evolqg" package - Melo *et al*, 2015). Partial Mantel tests with Phylogenetic Permutations were performed using the R functions multi.mantel ("phytools" package - Revell, 2012) to obtain residuals from regressions on phylogenetic distances and PhyloMantel ("evolqg" package) to carry out Harmon & Glor (2010)'s Phylogenetic Permutation tests.

Given recent criticisms of the Mantel test (e.g. Guillot & Rousset, 2013) and its low power in comparison to other methods in the context of comparative phylogenetic analyses (Harmon & Glor, 2010), we also employed alternative methods for Phylogenetic Signal Detection (K test - Blomberg *et al*, 2003; K-mult - Adams *et al*, 2014a) and for comparative phylogenetic analyses (PGLS $_{\lambda}$ - Freckleton *et al*, 2002; Revell, 2010; D-PGLS - Adams *et al*, 2014b) for Feliformia as a whole and one particular subgroup (family Herpestidae). The results with these methods were mostly consistent with our findings using the methods outlined above, and are described in **Appendix 16**. A more in-depth analysis of different Comparative Methods and techniques for identifying Phylogenetic Signal in studies of the evolution of morphological integration constitutes a promising avenue of study, and will be the focus of an upcoming study.

Character-specific evolutionary response patterns

We used Marroig *et al* (2011)'s Selection Response Decomposition (SRD) method to investigate character-specific covariance structure in greater detail for the set of 53 better-estimated taxa. SRD is an extension of the RS method in which response vectors (Δz) resulting from within-taxon **G** (or **P**) matrices subjected to random selection gradient vectors (β) are decomposed in character-specific vectors including direct (i.e. resulting from direct selection on the character) and indirect (i.e. resulting from selection on other correlated characters) responses to selection. Pairwise vector correlations between taxa of the character-specific response vectors resulting from this decomposition produce a distribution of correlations for each character, the average of which is referred to as the SRD score. In this work we used 2000 random selection vectors (taken from a normal distribution and standardised to a length of 1), producing distributions of 2000 correlations between character-specific response vectors and 35 character-specific SRD scores for each pairwise comparison, which were organised in 35 taxon-by-taxon matrices of "Similarity in Character Response Patterns" (SRDM).

Here we used the SRD test in three different ways. First, we performed significance tests to identify which characters had significantly different evolutionary response patterns for all pairwise comparisons, then calculated the proportion of significant results per character for all comparisons (i.e. within Feliformia as a whole), providing a general view of characters with the most divergent selection response

patterns. We also calculated the proportion of significant results for comparisons at other taxonomic levels; the results for these are shown in **Appendix 17**.

We also used Matrix Correlation and Mantel Tests to compare SRD score matrices for each character (SRDM) to the general Integration Pattern Similarity Matrix (IPSM) calculated using the RS method. This provides a measure of which characters are primarily responsible for the general structure of Integration Pattern variation between Feliform taxa (high similarity between SRDM and IPSM), and which tend to vary between species in their response patterns in ways that differ from the general trend of Integration Patterns.

Finally, we used Matrix Correlation and Mantel Tests to test for Phylogenetic Signal and to identify relationships to ecological factors (diet and sociality) in character-specific selection response patterns. Identification of Phylogenetic Signal was done by correlating the phylogenetic distance matrix (PDM) to the SRDM for each character. Tests for significant relationships between SRD Scores and ecological factors (DDM - diet and SDM - sociality) used partial Mantel Tests with Phylogenetic Permutations, as we were interested in relationships between response patterns and ecology independent of phylogenetic relatedness. The SRD analysis was performed using the corresponding function in the R package "evolqg"; Mantel Tests and partial Mantel Tests with Phylogenetic Permutations used the R packages "phytools" and "evolqg".

Results

Covariance matrix estimation and comparison of Integration Patterns

Raw and Adjusted similarity values and matrix repeatability for all pairwise comparisons between species-level matrices (n=63) and better-estimated matrices (n=53) are shown in **Appendix 18**. Matrix repeatability was >0.83 for most species-level matrices (except in 4 species) and >0.9 for most matrices from the set with sample sizes ≥ 17 (also except in 4 species). The minimum matrix repeatability values were 0.777 for *Leopardus tigrinus* and 0.797 for *Poiana richardsonii* (n=8 in both cases) in the species-level set, and 0.842 for *Eupleres goudotii* (n=18) and 0.856 for *Prionodon* (Genus - n=20). Lower repeatability was generally associated to matrices with smaller sample sizes, but sometimes higher values were found in species with lower sample size (e.g. *Prionailurus viverrinus*, t=0.894 with n=12 compared to *Hemigalus derbyanus*, t=0.889 with n=33).

Results of the rarefaction analysis using the *Felis catus + silvestris* matrix (**Figure 2-2**) show that similarity to the original matrix is very high for $n \geq 35$ (number of characters) and starts to drop more steeply approximately from $n = 20$. Similarity within families and within genera is very close, with a median of 0.81 and most values lying approximately between 0.75 and 0.85 in both cases. Similarity between different families is generally lower, with a median of 0.74 and most values standing between 0.65 and 0.80, approximately. Median similarity for matrices with $n \geq 16$ is higher than the median similarity of between-species comparisons within families and within genera, suggesting that results for all matrices in the dataset of 53 better-estimated matrices are likely to be reasonably reliable. The median similarity for $n \geq 12$ is higher than that for comparisons between species belonging to different families, suggesting that results for species in the dataset of 63 species-level matrices with $n < 12$ (*Poiana richardsonii*, *Prionodon pardicolor*, *Leopardus tigrinus*, *Leopardus colocolo*, *Galidictis fasciata*) might be misleading and should be interpreted with great care. The variance of values around the median starts increasing from approximately $n = 30$, and increases particularly rapidly as sample sizes get lower than $n = 19$. The results above indicate that the inclusion of 5 matrices with relatively low sample sizes ($17 \leq n \leq 35$) in the set of better-estimated matrices may be justified in order to allow the analyses to include all Feliform families and subfamilies, although the results for taxa with low sample sizes must be analysed with care. Results of rarefaction analyses with species having less variation explained by the first principal component show relatively greater drops in similarity to the original matrix with decreasing sample sizes. However, the similarities between the original matrix and matrices estimated with $n \geq 17$ are still always higher than the median similarity for within-family and within-genus comparisons (**Appendix 6**).

Mean pairwise adjusted similarity in integration patterns was similarly high for comparisons among the 63 species-level matrices (mean = 0.734) and the 53 better-estimated matrices (mean = 0.777). The highest similarities were found for comparisons between felids (*Caracal caracal* vs *Leopardus mitis* = 0.944; *C. caracal* vs *Prionailurus bengalensis* = 0.936) and also between two convergent species, the African palm civet (*Nandinia binotata*, family Nandiniidae) and one of the Asian palm civets (the viverrid *Paradoxurus musanga*; similarity of 0.936). Minimum similarities in the 63 species-level matrix dataset were quite low, and as expected mostly involved species with very low sample sizes and low repeatability, such as the spotted linsang *Prionodon*

pardicolor (*Pr. pardicolor* vs *Leopardus colocolo*, 0.277; *Pr. pardicolor* vs *Prionodon linsang*, 0.288; *Pr. pardicolor* vs *Panthera tigris*, 0.281). The lowest similarities in the set of 53 better-estimated matrices are less extreme (*Prionodon* (Genus) vs *Panthera leo*, 0.473; *Prionodon* (Genus) vs *Neofelis* (Genus), 0.504; *Prionodon* (Genus) vs *Salanoia concolor*, 0.506). Comparisons showing the least similarity for the better-estimated matrices still involve the linsangs, with small sample sizes (*Prionodon*, n=20, mean similarity = 0.590). The clades with lowest sample sizes show mean similarities comparatively higher than that of *Prionodon* (*Salanoia concolor*, n=17 and *Eupleres goudotii*, n=18; mean similarities of 0.746 and 0.670, respectively). The mean similarity of *Salanoia concolor*, particularly, is higher than the lowest mean similarities for taxa with $n \geq 35$ (*Parahyaena brunnea*, n=48, mean similarity 0.7101; *Suricata suricatta*, n=49, mean similarity 0.7120). While *Prionodon*'s relatively low sample size still casts some doubt on the validity of the integration patterns estimated here for this taxon, the results above suggest that *Prionodon*'s distinctive integration pattern may in fact be at least in part representative of their biology and not simply reflect its low sample size.

Figure 2-3 shows the result of pairwise comparisons and the distribution of the 63 species-level matrices in the integration space created by a PCO on RS values. The heatmap (**Figure 2-3A**) suggests higher similarities among some groups (mostly Felids and Viverrids), and makes clear the overall lower similarity of some less well-sampled species. The distribution in the Integration Space comprised of the two first PCO axes of matrix similarity (**Figure 2-3B**, explaining 34.21% of total variation) shows a grouping of most felids, separate from Herpestids, Viverrids and Euplerids, reflecting results seen in the heatmap. The low overall similarity of species with low sample size does not always translate to large deviations from other species within the same family in the integration space: the positions of *Prionodon pardicolor* and *Leopardus tigrinus* seem clearly aberrant, but other species with small samples are less atypical, such as *Prionodon linsang* (positioned relatively closer to members of Viverridae and Herpestidae), *Prionailurus viverrinus* (nested among other felids) and *Poiana richardsonii*. Although the very low sample size of the African linsang (*Poiana richardsonii*) casts doubts on the validity of this observation, it is interesting that the integration pattern of *P. richardsonii* seems to be closer to that of other Viverrids like *Genetta servalina* and *Viverricula indica* than to the *Prionodon* species which their morphology closely resembles.

Pairwise comparisons and the distribution in Integration Space for the 53 better-estimated matrices are shown in **Figure 2-4**. The heatmap (Figure 2-4A) once again plainly shows two sets of higher similarities: among Felids; and among most Viverrids, Herpestids and Euplerids. With overall low similarities, the *Prionodon* matrix is now clearly the most deviant, apparently differing even more from its sister-group Felidae than from other families.

Some finer-scale details can also be observed in the heatmap: some Felids have distinctly lower similarity to others in the family (*Puma concolor*; *Leopardus tigrinus* group; *L. wiedii* and *Panthera uncia*); high similarity is seen among the three larger hyaenas (*Crocuta crocuta*, *Hyaena hyaena* and *Parahyaena brunnea* - subfamily Hyaeninae), but not the Aardwolf (*Proteles cristata*); some taxa besides *Prionodon* have relatively low overall similarities (*Salanoia concolor* and *Eupleres goudotii*, but also taxa with larger samples like *Hemigalus derbyanus* and *Genetta servalina*); the African (*Nandinia binotata*) and Asian (*Paradoxurus musanga*) palm civets and the fossa (*Cryptoprocta ferox*) share high similarities among themselves and with felids.

Figure 2-2. Rarefaction analysis from 115 to 3 individuals on a pooled *Felis catus* + *Felis silvestris* **P** matrix and distribution of pairwise similarities within different taxonomic levels (between families, within families and within a genus), using the Random Skewers (RS) method. The horizontal line indicates the median value of pairwise similarities within families. Vertical lines indicate the distribution of similarities for $n=35$ (number of characters), $n=17$ and $n=7$ (minimum sample sizes here for better-estimated matrices and for species-level matrices).

Figure 2-3. Pairwise comparisons (RS) between the 63 species-level matrices (A) and position of each in the Integration Space defined by the 2 first Principal Coordinates of Integration Pattern Similarity for the species-level matrices.

Figure 2-4. Pairwise comparisons (RS) between the 53 better-estimated matrices (A) and position of taxa in the Integration Space defined by the 2 first Principal Coordinates of Integration Pattern Similarity for the better-estimated matrices.

The Integration Space represented by the two first PCO axes of Matrix Similarity for 53 taxa (**Figure 2-4B**, explaining 39.03% of total variation) shows a reordering compared to that for the species-level matrices, likely due to the removal of poorly estimated taxa, but keeps a general division in two main groups (Felids vs other families). Some features of Integration Pattern variation can be seen here in greater detail. Herpestids and Viverrids have partially overlapping integration patterns, but parts of the integration space represented by the two first PCO axes are occupied exclusively by one of these families (e.g. *G. servalina* for Viverrids and *Crossarchus* for Herpestids). With very high values on PCO2, the subfamily Hyaeninae has a relatively distinct integration pattern, apparently similar to that of *Salanoia concolor*, but different from all other taxa, whereas the insectivorous Aardwolf (*Proteles cristata*) shows a pattern akin to Viverrids, Herpestids and Euplerids. The palm civets (*Nandinia binotata* and *Paradoxurus musanga*) lie on the edge of the Integration Space occupied by felids, and the fossa (*Cryptoprocta*) sits right amidst other Felids, apparently sharing an Integration Pattern similar to members of that family. Felids with lower similarity to other species in the family according to the heatmap (*Puma concolor*; *Leopardus tigrinus* group; *L. wiedii* and *Panthera uncia*) are located at the left edge of the Integration Space for the group. Finally, *Prionodon*, in accordance with its very low similarity to other groups, lies in a position distant from all other taxa, but closer to Viverrids and particularly distant from their sister group Felidae.

Integration Magnitudes and Isometric Variation

Table 2-2 shows the correlations found between metrics of Integration Magnitude (r^2 , ICV), size variation (%PC1, % isometric variation) and evolutionary metrics (flexibility - $\bar{f}$ and constraints). Metrics for Integration Magnitude and size variation are highly positively correlated, indicating a high contribution of size variation to overall integration and also that the % PC1 apparently provides a rather accurate estimation of actual variation in isometric size for Feliform skulls. Size variation and Integration Magnitudes are also positively correlated to constraints (average alignment between selection response and the direction of PC1) and negatively correlated to flexibility ($\bar{f}$ - average alignment between selection response and the direction of selection).

Since Marroig *et al* (2009)'s constraints are defined based on the alignment between selection response and PC1, the high correlation between size variation and

constraints is a consequence of PC1 aligning closely with isometric size in most Feliforms. Accordingly, constraints are low in taxa with lower %PC1 and also in those in which PC1 is less aligned to isometry. (**Figure 2-5**).

Table 2-2. Correlations between Integration Magnitude indexes (r^2 , ICV), percentage of variation represented by PC1 (%PC1), percentage of isometric variation, and evolutionary metrics (flexibility ($\bar{F}$) and Constraints - Marroig *et al.*, 2009).

	r^2	ICV	%PC1	% iso	$\bar{F}$
r^2					
ICV	0.972				
%PC1	0.961	0.991			
% iso	0.961	0.947	0.963		
$\bar{F}$	-0.941	-0.980	-0.958	-0.902	
constraints	0.887	0.926	0.966	0.943	-0.879

Despite some differences concentrated among intermediate values, the distributions of bootstrapped Integration Magnitude (r^2) and percentages of isometric variation (**Figure 2-6**) show a shared general pattern, as expected given the high correlation between these variables. Actual observed values show wide variation, from 0.071 in *Crossarchus* to 0.399 in *Panthera leo* for r^2 , and likewise from 11.15% (in *Prionodon*) to a maximum of 56.45% (in *P. leo*) in the proportion of isometric variation. The presence of a lower proportion of isometric variation in *Prionodon* despite its relatively higher r^2 is likely a result of PC1 not representing a size vector in this taxon (correlation PC1 x isometry ~ 0.2 , as seen in Figure 2-5). For *Prionodon*, the second and third principal components are more highly correlated to isometry (PC2 x isometry = 0.55; PC3 x isometry = 0.45).

Figure 2-5. Relationship between PC1 - Isometry alignment (PC1 x isometry), percentage of variation in PC1 (%PC1) and Constraints among Feliforms.

Interestingly, isometric variation and r^2 show trends associated to the different Feliform families: most remarkably, Felidae tends to show high to very high size variation and integration, whereas *Nandinia* has high values, similar to some Felids, Viverrids and Herpestids have mostly low or intermediate values, and Prionodontidae and all four Hyaenidae have low integration and a small proportion of isometric variation. For Euplerids, three species show values comparable to Viverrids and Herpestids, *Eupleres goudotii* has relatively low values and *Cryptoprocta* has very high integration and proportional isometric variation, approximating that found in the most integrated Felids. Despite these general patterns, low integration values do occur in some Felidae (particularly in *Leopardus tigrinus* group, *L. wiedii* and *Panthera uncia*), and high integration and isometric variation are found in a Viverrid (the Asian palm civet *Paradoxurus musanga*).

Figure 2-6. Distribution of bootstrapped Integration Magnitude (r^2) values (A) and percentage of isometric variation (B) for the 53 Feliform taxa with better-estimated matrices.

Figure 2-7 shows Integration Magnitude (r^2) for the seven Feliform families and for different mammalian families (Porto *et al*, 2009). The total r^2 range for Feliformia is remarkably wide, including values similar to those for some apes (*Pan*, *Gorilla*) in *Crossarchus* on the low end, up to values found among the most highly integrated marsupials (Diprotodontia) in *P. leo*. Mean integrations for Felidae and the value for the monospecific Nandiniidae approximate the r^2 found in Dasyuromorphia, Hyracoidea and the primate *Papio*, whereas the values in Hyaenidae and *Prionodon* (slightly lower than the averages for Herpestidae and Viverridae, families with

considerable variation) approximate those for Artiodactyla and Perissodactyla. The high average r^2 for Eupleridae is driven by *Cryptoprocta*'s extremely high value; as seen in Figure 2-6, most malagasy carnivores have similar values to most Herpestidae and Viverridae. The r^2 for the Carnivoran included in Porto *et al* (2009)'s work (the canid *Cerdocyon thous*) is similar to that for *Nandinia* and the average for Felids, and therefore higher than most values for other Feliformia.

Figure 2-7. Average (in gray) and range of Integration Magnitude (r^2) values found for each family of Feliformia in this study and r^2 values for representatives of various mammalian orders in Porto *et al*, 2009 (in black).

Integration, size, phylogenetic, morphological and ecological distances - Comparative Methods

Table 2-3 shows the results of Mantel Tests and Partial Mantel Tests with Phylogenetic Permutations for Feliformia and less inclusive phylogenetic groupings within the suborder. For the suborder as a whole, all factors but sociality are significantly correlated to phylogeny, the highest strength of association being found for Integration Patterns (IP). Integration Patterns and Magnitudes (r^2) and Morphology (MD) are correlated within the suborder both before and after correcting for phylogenetic relatedness, implying that Pattern and Magnitudes of morphological integration tend to change in a coordinated way, and that these changes tend to follow differences in average morphology both between and within groups. The high correlation between size and morphology is unsurprising, since morphological distances here include skull size differences. In fact, the first PCO axis of morphological distances is highly correlated to skull size ($r = 0.95$; $p < 2.2 \times 10^{-16}$). The correlations of skull size to Integration Patterns and Magnitude, however, indicate that changes in Integration tend to accompany differences both in absolute skull size and also in other aspects of average morphology (since the correlation between morphological distances and integration is higher than that between skull size and integration). When not correcting for phylogenetic signal, diet shows a small, but significant correlation with Integration Patterns and Morphology for the whole suborder (for $\alpha=0.10$ for the latter); however, these effects disappear after correcting for phylogenetic relatedness. Sociality, on the other hand, correlates significantly with size and morphology, but not with Integration.

Significant correlations of Integration Patterns and Magnitudes to phylogeny are found for most less-inclusive groupings above the family level (signal is found only for Patterns in Viverroidea and Hyaenidas + Herpestidae + Eupleridae, and the correlation is small and significant for $\alpha=0.10$ only for the former), but for none at the family or subfamily levels. The absence of phylogenetic effects at family and subfamily levels might be an artefact of sample sizes, as lower-level groups include gradually smaller numbers of species; nonetheless, this does not seem to be the case given the very low correlations between phylogeny and IP/ r^2 for all subfamilies and families, except for Eupleridae, where a moderate correlation (0.545) is found between r^2 and phylogeny, but considered non-significant because of the small number of taxa in the clade (5 taxa).

Table 2-3. Mantel tests and partial Mantel tests with phylogenetic permutations (Harmon & Glor, 2010) between integration patterns (IP) and magnitudes (r^2), morphology (Mahalanobis distance, MD), size (log gm) and ecology (diet - DD and sociality - SD) for Feliformia and internal taxonomic groups within the suborder. Species sample size (n) is indicated for each group. Significance indicated by underlined values in **bold** ($\alpha=0.05$) and *italic* ($\alpha=0.10$).

Feliformia (n=50)	IP	r^2	MD	Size	DD	SD
Phylogeny	<u>0.431</u>	<u>0.253</u>	<u>0.329</u>	<u>0.156</u>	<u>0.377</u>	-0.006
Pattern (IP)		<u>0.339</u>	<u>0.334</u>	<u>0.259</u>	<u>0.158</u>	0.081
IP*		<u>0.264</u>	<u>0.225</u>	<u>0.215</u>	-0.005	NA
Magnitude (r^2)			<u>0.253</u>	<u>0.194</u>	0.006	0.104
r^2 *			<u>0.185</u>	<u>0.162</u>	NA	NA
Morphology (MD)				<u>0.775</u>	<i><u>0.107</u></i>	<u>0.334</u>
MD*				<u>0.775</u>	-0.019	<u>0.356</u>
Size					0.003	<u>0.322</u>
Size*					NA	<u>0.327</u>
Diet (DD)						-0.027
DD*						NA
Felidae (n=22)	IP	r^2	MD	Size	DD	SD
Phylogeny	0.028	0.068	<u>0.278</u>	<u>0.346</u>	<u>0.128</u>	-0.036
Pattern (IP)		<u>0.453</u>	<u>0.353</u>	<u>0.380</u>	0.020	0.111
IP*		<u>0.452</u>	<u>0.359</u>	<u>0.394</u>	NA	NA
Magnitude (r^2)			<u>0.378</u>	<u>0.320</u>	0.021	<i><u>0.270</u></i>
r^2 *			<u>0.375</u>	<u>0.316</u>	NA	<u>0.273</u>
Morphology (MD)				<u>0.901</u>	0.050	<u>0.492</u>
MD*				<u>0.893</u>	NA	<u>0.523</u>
Size					<u>0.218</u>	<u>0.285</u>
Size*					<u>0.186</u>	<u>0.317</u>
Diet (DD)						-0.082
DD*						NA
Pantherinae (n=6)	IP	r^2	MD	Size	DD	SD
Phylogeny	-0.293	-0.243	-0.020	0.237	-0.339	-0.301
Pattern (IP)		0.696	-0.191	-0.199	-0.104	-0.208
IP*		0.673	NA	NA	NA	NA
Magnitude (r^2)			0.076	0.003	-0.412	0.254
r^2 *			NA	NA	NA	NA
Morphology (MD)				<u>0.842</u>	-0.459	0.513
MD*				0.872	NA	0.531
Size					-0.384	0.120
Size*					NA	NA
Diet (DD)						-0.331
DD*						NA
Feloidea (n=23)	IP	r^2	MD	Size	DD	SD
Phylogeny	<u>0.821</u>	<u>0.253</u>	<i><u>0.277</u></i>	<u>0.388</u>	0.009	-0.095
Pattern (IP)		<u>0.450</u>	<i><u>0.363</u></i>	<u>0.458</u>	-0.001	-0.008
IP*		<u>0.437</u>	<u>0.246</u>	<u>0.264</u>	NA	NA
Magnitude (r^2)			<u>0.416</u>	<u>0.387</u>	0.021	<i><u>0.236</u></i>
r^2 *			<u>0.372</u>	<u>0.510</u>	NA	<u>0.271</u>
Morphology (MD)				<u>0.905</u>	0.070	<u>0.462</u>
MD*				<u>0.901</u>	NA	<u>0.510</u>
Size					<u>0.222</u>	<i><u>0.252</u></i>
Size*					<u>0.237</u>	<u>0.315</u>
Diet (DD)						-0.059
DD*						NA
Felinae (n=16)	IP	r^2	MD	Size	DD	SD
Phylogeny	-0.137	-0.111	0.083	0.041	0.025	-0.044
Pattern (IP)		<i><u>0.285</u></i>	<i><u>0.351</u></i>	<u>0.383</u>	0.028	0.157
IP*		<u>0.274</u>	<u>0.367</u>	<u>0.392</u>	NA	NA
Magnitude (r^2)			-0.133	-0.006	<u>0.275</u>	-0.208
r^2 *			NA	NA	<u>0.280</u>	NA
Morphology (MD)				<u>0.866</u>	0.127	<i><u>0.384</u></i>
MD*				<u>0.867</u>	NA	<i><u>0.390</u></i>
Size					<i><u>0.160</u></i>	0.187
Size*					<i><u>0.159</u></i>	<i><u>0.190</u></i>
Diet (DD)						-0.007
DD*						NA
Viverroidea (n=26)	IP	r^2	MD	Size	DD	SD
Phylogeny	<i><u>0.125</u></i>	0.013	<u>0.300</u>	<u>0.258</u>	<u>0.172</u>	-0.039
Pattern (IP)		0.218	<u>0.321</u>	<u>0.204</u>	0.023	0.073
IP*		NA	<u>0.338</u>	<i><u>0.221</u></i>	NA	NA
Magnitude (r^2)			-0.095	-0.075	-0.092	0.031
r^2 *			NA	NA	NA	NA
Morphology (MD)				<u>0.871</u>	0.077	<u>0.292</u>
MD*				<u>0.873</u>	NA	<u>0.318</u>
Size					0.036	<u>0.293</u>
Size*					NA	<u>0.321</u>
Diet (DD)						-0.086
DD*						NA

Table 2-3 (cont.). Mantel tests and partial Mantel tests with phylogenetic permutations (Harmon & Glor, 2010) between integration patterns (IP) and magnitudes (r^2), morphology (Mahalanobis distance, MD), size (log gm) and ecology (diet - DD and sociality - SD) for Feliformia and internal taxonomic groups within the suborder. Species sample size (n) is indicated for each group. Significance indicated by underlined values in **bold** ($\alpha=0.05$) and *italic* ($\alpha=0.10$).

Viverridae (n=11)	IP	r^2	MD	Size	DD	SD
Phylogeny	0.014	-0.026	0.447	0.292	<i>0.198</i>	NA
Pattern (IP)		0.224	0.112	0.074	0.237	NA
IP*		NA	NA	NA	NA	NA
Magnitude (r^2)			-0.185	-0.228	-0.109	NA
r^2 *			NA	NA	NA	NA
Morphology (MD)				0.699	<i>0.248</i>	NA
MD*				0.665	0.182	NA
Size					0.135	NA
Size*					NA	NA
Diet (DD)						NA
DD*						NA
HeEu (n=13)	IP	r^2	MD	Size	DD	SD
Phylogeny	0.243	0.301	0.595	0.152	0.020	0.035
Pattern (IP)		0.298	0.456	-0.053	-0.066	-0.013
IP*		0.243	0.399	NA	NA	NA
Magnitude (r^2)			<i>0.396</i>	<i>0.471</i>	-0.019	0.034
r^2 *			0.283	0.451	NA	NA
Morphology (MD)				0.587	0.049	0.114
MD*				0.626	NA	NA
Size					0.121	0.049
Size*					NA	NA
Diet (DD)						0.134
DD*						NA
HyHeEu (n=17)	IP	r^2	MD	Size	DD	SD
Phylogeny	0.281	0.118	0.664	0.637	<i>0.147</i>	0.008
Pattern (IP)		0.264	<i>0.313</i>	0.173	0.076	0.013
IP*		NA	0.176	NA	NA	NA
Magnitude (r^2)			-0.073	-0.041	-0.041	0.014
r^2 *			NA	NA	NA	NA
Morphology (MD)				0.913	<i>0.202</i>	0.162
MD*				0.850	0.140	NA
Size					<i>0.171</i>	0.125
Size*					0.101	NA
Diet (DD)						0.014
DD*						NA
Herpestidae (n=9)	IP	r^2	MD	Size	DD	SD
Phylogeny	-0.066	-0.296	0.282	0.152	0.307	0.499
Pattern (IP)		0.004	0.056	-0.330	0.097	0.221
IP*		NA	0.078	NA	0.123	0.294
Magnitude (r^2)			-0.226	-0.334	0.033	-0.031
r^2 *			NA	NA	NA	NA
Morphology (MD)				0.707	0.495	0.370
MD*				0.701	0.447	0.276
Size					0.411	0.055
Size*					0.387	NA
Diet (DD)						0.199
DD*						<i>0.055</i>
Eupleridae (n=5)	IP	r^2	MD	Size	DD	SD
Phylogeny	0.144	0.545	0.931	0.686	0.256	NA
Pattern (IP)		0.297	0.428	-0.008	-0.326	NA
IP*		0.264	0.817	NA	NA	NA
Magnitude (r^2)			<i>0.657</i>	0.764	-0.334	NA
r^2 *			0.488	0.640	NA	NA
Morphology (MD)				0.710	0.066	NA
MD*				0.271	NA	NA
Size					-0.143	NA
Size*					NA	NA
Diet (DD)						NA
DD*						NA

An association between Integration Patterns and Magnitudes is found within Feloidea (Felidae + Prionodontidae), Felidae, the subfamily Felinae, and also within Herpestidae + Eupleridae after correcting for phylogenetic relatedness. Average morphology and size are correlated to Integration Patterns within Feloidea, Felidae, Felinae and Viverroidea. In Hyaenidae + Herpestidae + Eupleridae, Herpestidae + Eupleridae and Herpestidae, average morphology also correlates to integration patterns (but size does not). Additionally, average morphology and size are correlated to Magnitudes of Integration (r^2) in Feloidea, Felidae, and Herpestidae + Eupleridae; in Eupleridae, morphology (but not size) correlates to r^2 only after correcting for phylogenetic signal. These results show that links between Patterns and Magnitudes of Integration, and also between average morphology and Integration, are widespread within the suborder, even if not general for the group as a whole. Although the correlation between Magnitudes and Patterns was not significant for Pantherinae (species sample size of 6 only), the rather high correlation found within this groups (0.696) might indicate a general relation between Patterns and Magnitudes of Integration at least within Feloidea.

Regarding ecological factors, diet is found to correlate to average body size (log gm) in many less-inclusive feliform groups (Feloidea, Felidae, Felinae, Herpestidae; also Hyaenidae + Herpestidae + Eupleridae before correcting for phylogenetic relatedness, likely reflecting differences between Hyaenidae and the other two families). Diet also correlates to average morphology in Viverridae and Hyaenidae + Eupleridae (only before correcting for phylogenetic signal), as well as in Herpestidae (also after correcting for phylogenetic signal). Though not widespread, associations between Diet and Integration are found in two cases: for Magnitudes (r^2) in the subfamily Felinae (small cats), and for Integration Patterns in the mongooses (Herpestidae - only after correcting for phylogenetic relatedness). Social behaviour is linked to size and average morphology in Felidae, Felidae, Felinae and Viverroidea. For Herpestidae, remarkably, sociality is linked to average morphology (but not size), and also to Integration Patterns, showing that a relationship between social behaviour and morphological integration exists at least for this clade.

Character-specific evolutionary response patterns

The proportion of significant differences character-specific selection response patterns for comparisons at different taxonomic levels are shown in **Appendix 17**. For Feliformia as a whole, we represent the proportion of significant differences for each character on a *Panthera onca* skull in **Figure 2.8A**, along with correlations between character-specific response patterns (SRD values) and general integration patterns calculated by the Random Skewers method (**Figure 2.8B**). Significantly different response patterns occur mostly for characters at the skull vault (BR-LD, LD-AS, JP-AS, BR-PT; also PT-TSP which lies between the vault and zygomatic arch), APET-TS and BA-OPI at the base of the skull and, less frequently, for some characters at the zygomatic arch (EAM-ZYGI, ZS-ZI; ZI-MT. The oral and nasal regions tend to have more similar responses between species. Generally, the highest correlation between character-specific responses and general integration patterns are found for characters with more similar responses between species (particularly characters in the facial region), whereas characters with response patterns often varying between species tend to be less correlated with general integration patterns (the main exception being APET-TS). This suggests that most characters with response patterns often differing between species may vary in ways that are inconsistent with the general integration pattern similarity represented by the Random Skewers metric.

Matrix correlations between character-specific response patterns (SRD values) and phylogeny (A, significance based on Mantel Tests), as well as diet (B) and sociality after correcting for phylogenetic relatedness (C, significance for B and C based on partial Mantel Tests with Phylogenetic Permutations) are shown in **Figure 2-9** for Feliformia as a whole and in **Figure 2-10** for the family Herpestidae, which showed links between Integration Patterns and both Diet and Sociality in comparative analyses.

Within Feliformia as a whole, phylogenetic effects are widespread among facial characters and are also found on some characters at the skull base (BA-EAM) and vault (e.g. PT-BA, PT-EAM, BR-APET); in Herpestidae, conversely, significant phylogenetic effects are found only for OPI-LD, at the skull vault. Correlations between selection response patterns and diet are relatively widespread for Feliformia as a whole and even more so for Herpestidae, and occur in many facial characters (especially, but not only in the zygomatic region), but also at the vault (e.g PT-EAM; JP-AS; OPI-LD for Feliformia as a whole; PT-BA; PT-BR for Herpestidae). Few effects related to social behaviour are recognised for Feliformia as a whole. Those that were identified include

not only part of the skull vault (PT-BA, PT-AS), as would be expected according to the social brain hypothesis, but also the zygomatic arch (ZI-ZYGI, ZS-ZI) and other facial characters (e.g. MT-PNS, IS-PNS, PM-MT). Sociality effects are more common and widespread among mongooses (Herpestidae), affecting characters at the vault, but also at the skull base (APET-BA), the zygomatic arch (PT-ZYGI, ZYGI-TSP, ZI-ZYGI) and parts of the nasal and oral regions - including characters also correlated to dietary variation.

Figure 2-8. Proportion of significant pairwise between-species comparisons of character-specific evolutionary response patterns (SRD - Selection Response Decomposition) for Feliformia (A) and Matrix Correlation between character-specific evolutionary response patterns (SRD values) and general Integration Pattern measured by the Random Skewers method (B), shown on a representation of a *Panthera onca* skull. Mantel tests of the correlation between SRD and RS is significant at $\alpha=0.05$ for all characters but PT-TSP ($p=0.088$); nonetheless, characters most often showing significant differences are those less related to the general Integration Pattern, and vice-versa.

Figure 2-9. Character-specific evolutionary response patterns (SRD)'s correlations with phylogeny (A) and partial correlations between SRD and diet (B) and social behaviour (C) for Feliformia as a whole, drawn on representations of a jaguar (*Panthera onca*) skull. Colour indicates correlation values; line widths indicate Mantel test significance levels (very thin lines = nonsignificant; medium lines = significant at $\alpha=0.10$; thick lines = significant at $\alpha=0.05$; very thick lines = significant at $\alpha=0.05$ with bonferroni correction for 35 tests). Significance tests of SRD x Diet and SRD x Sociality are based on partial Mantel Tests with Phylogenetic Permutations

Figure 2-10. Character-specific evolutionary response patterns (SRD)'s correlations with phylogeny (A) and partial correlations between SRD and diet (B) and social behaviour (C) for the family Herpestidae, drawn on representations of a meerkat (*Suricata suricatta*) skull. Colour indicates correlation values; line widths indicate Mantel test significance levels (very thin lines = nonsignificant; medium lines = significant at $\alpha=0.10$; thick lines = significant at $\alpha=0.05$; very thick lines = significant at $\alpha=0.05$ with bonferroni correction for 35 tests). Significance tests of SRD x Diet and SRD x Sociality are based on partial Mantel Tests with Phylogenetic Permutations.

Discussion

Despite its vast significance for phenotypic micro- and potentially also macroevolution (Bolstad *et al*, 2014), the evolutionary change of morphological integration is still an open question which has only recently started to be examined in greater detail (Marroig & Cheverud, 2001; Goswami, 2006a; Porto *et al*, 2009; Oliveira *et al*, 2009; Haber, 2015). Here we carried out the most taxonomically diverse comparative investigation of phenotypic integration in feliform carnivoran skulls to date, finding integration patterns to be generally rather similar, as shown in previous works on mammals (Marroig & Cheverud, 2001; Goswami, 2006a; Oliveira *et al*, 2009; Porto *et al*, 2009). Differently from most previous works, we found differences in integration patterns to be roughly structured according to phylogenetic groups (with disparities between Felids, Hyaenids, Viverrids/Herpestids and *Prionodon*), and identified coordinated changes of average skull morphology, integration patterns and magnitudes of integration at least in part of the Feliformia evolutionary history, leading to remarkably similar integration patterns in morphologically convergent, but phylogenetically distant clades such as felids and fossas (*Cryptoprocta*, family Eupleridae) and Asian and African palm civets (*Nandinia binotata*, family Nandiniidae and *Paradoxurus musanga*, family Viverridae). By partitioning isometric size variation and calculating its contribution to total variation in each taxon, we explicitly show that many felids - but also *Cryptoprocta*, *Nandinia* and *Paradoxurus musanga* - have enormous amounts of their total within-population variation represented by isometric size changes alone. We identified a previously unrecognised role of diet as a factor shaping morphological integration patterns within Feliformia as a whole and one of its families (Herpestidae), and also influencing integration magnitudes in small cats (subfamily Felinae). We also show for the first time that social behaviour may be a driver of changes in morphological integration, at least for mongooses (Herpestidae) and/or within the selection response patterns of particular characters within the skull.

Most previous works on the evolution of phenotypic integration in mammals have revealed general similarity in integration pattern both within particular groups (Platyrrhini primates, Marroig & Cheverud, 2001; Carnivora, Goswami, 2006a; Catarrhini primates, Oliveira *et al*, 2009; Xenarthra, Hubbe, 2013; Sigmodontine rodents, Costa, 2013; Phyllostomid bats; Rossoni, 2013) and between representatives of different orders (Porto *et al*, 2009), interpreted as a possible evidence of internal

stabilizing selection maintaining the stability of inter-trait relationships (Cheverud, 1996a; Marroig & Cheverud, 2001). Internal stabilizing selection could result from a requirement of structural cohesion within organisms, and is reflected for instance in shared developmental patterns in mammal skulls - Smith, 2001; Gross & Hanken, 2008; Richtsmeier & Flaherty, 2013; Koyabu *et al*, 2013). Our results equally show high overall similarity between covariance matrices, and therefore may be seen as further evidence of generally stable inter-trait relationships in mammals, resulting from shared developmental patterns.

Haber (2015) also finds similarly-valued integration pattern similarities among ruminants to those found in the previous works mentioned above, with covariance matrix similarities greater than 0.7 even between different families. At the same time, she recognises a split in morphological integration patterns between the families Cervidae and Bovidae, with variation relatively constrained within each family. While some previous results had already shown associations between integration patterns and phylogeny (Goswami, 2006a; Oliveira *et al*, 2009; Hubbe, 2013), Haber (2015)'s work is the first to call attention to differences in integration patterns occurring specifically in the split between two phylogenetic groups. Although the methods used by her differ from those employed here, our data suggest a similar structuring of (generally similar) integration patterns between phylogenetic or taxonomic groups. The integration space built by the first axes of a PCoA on pattern similarities for the 53 better-estimated matrices (representing 39.03% of total variation in integration patterns) shows relatively well-structured separations between at least four groups: Felidae and Prionodontidae appear at opposite extremes of the integration space, whereas Herpestids and Viverrids show some overlap, and among Hyaenidae the three bone-cracking hyaenas (Hyaeninae) also tend to group separately from other taxa. The five Malagasy carnivores (Eupleridae) with better-estimated matrices show a spread in integration space similar or higher to that of more speciose families. This last fact in part seems to reflect a tendency of morphologically convergent species to also show convergent phenotypic integration patterns in our data: patterns show remarkable similarity between the palm civets *Nandinia binotata* (Nandiniidae, African) and *Paradoxurus musanga* (Viverridae, Asian), between the malagasy ring-tailed mongoose *Galidia elegans* (Eupleridae) and other mongooses (family Herpestidae) and between the cat-like fossas (*Cryptoprocta*, Eupleridae, Madagascar) and other Felidae. Also, the integration pattern of the Aardwolf (*Proteles cristata*), a hyaenid insectivore specialised in termites,

is closer to that of viverrids and herpestids than to the bone-cracking Hyaenas. Such convergences in integration patterns following morphological similarities do not seem to be a general rule within Feliformia, however. The malagasy civet (*Fossa fossana*, Eupleridae) does not show an integration pattern particularly similar to that of other civets (Viverridae), and even though the matrix estimated for the African linsang (*Poiana richardsoni*) is quite unreliable due to its very low sample size, our estimate of the phenotypic integration pattern for this species seems to group with other viverrids rather than with the distinctive pattern of the Asian linsangs (Prionodontidae). Although this integration space expresses less than a half of the total variance, it represents relevant variations existing in integration patterns. Furthermore, the structuring in groups identified is also consistent with results obtained for the associations between integration, average morphology and phylogeny, as discussed below.

Interestingly, we found an almost perfect mismatch between the characters most often showing divergent responses to selection between species according to the SRD method (Marroig *et al*, 2011), mostly concentrated at the skull vault and also including some characters at the basicranium and zygomatic subregion, and those guiding overall similarities in integration patterns (as measured by the Random Skewers method), which include most characters at the face, and also some at the skull base and vault. This mismatch implies that the most divergent characters, while showing ample variation in their responses to selection, do so in a way that is relatively independent from the rest of the skull, and therefore do not reflect more general dissimilarities in skull integration.

Our explicit calculation of the proportion of total variation represented by isometric size variation (%isometry) showed that, for feliforms, the amount of isometric variation is highly correlated to the proportion of variation represented by the first principal component (%PC1) of the **P** matrix - although the actual correlation between the isometric vector and the first eigenvector of **P** (in the log scale) was low or relatively low for some taxa (*Parahyaena brunnea*, *Genetta servalina*, *Eupleres goudotii*, *Prionodon*). This shows that, although the PC1 of interlandmark distances is generally not strictly isometric (Jolicœur, 1963; Somers, 1986), and in fact is not always strictly size-related (e.g. many species in Rossini, 2013; *Prionodon* here), its use as a surrogate for size is in most cases justified within Feliformia, unless one is specifically interested in questions related to isometry and allometry.

The relationships between %PC1, indexes of integration magnitude (r^2 , ICV) and evolutionarily relevant metrics (flexibility, constraints) identified in Marroig *et al* (2009) are shown here to be equally valid within Feliformia. The proportion of isometric variation is also shown to have a very strong positive association with the magnitude of integration. Consequently, the proportion of isometric variation within populations has high evolutionary relevance in itself, as taxa with higher proportions of isometric variation display lower evolutionary flexibility (and likewise higher constraints, as defined in Marroig *et al*, 2009) and therefore tend to produce selection responses more often aligned to a size-related direction instead to the actual direction of selection. Of course, conversely, in situations where the direction of selection is itself aligned to isometric size, highly integrated taxa with large proportions of isometric variation can show particularly strong responses aligned to selection. We show that this situation of high isometric size variation and integration, and therefore lower evolutionary flexibility, seems to be the rule for most Felids, as well as some other taxa.

Felids are traditionally considered to have relatively low between-species shape disparity, but large size differences (e.g. Kitchener *et al*, 2010; Sicuro & Oliveira, 2011). Our results show that most taxa in this family also show an outstanding amount of within-population isometric variation, often surpassing 40% of total variation and falling slightly short of 60% in lions (*Panthera leo*), tigers (*P. tigris*), leopard cats (*Neofelis*) and pumas (*Puma concolor*) - but also in the cat-like fossas (*Cryptoprocta ferox* - family Eupleridae). Size variation thus makes up not only the most of between-species variation, but also a large amount of within-population variation for most felids, as well as one taxon often recognised as a cat-like ecomorph (Van Valkenburgh, 2007). Some other non-felid taxa also show considerably high proportions of isometric variation, as is the case for the palm civets *Nandinia binotata* (Nandiniidae) and *Paradoxurus musanga* (Viverridae). On the other hand, some felids, like *Panthera uncia*, *Leopardus wiedii* and the *L. tigrinus* group display a lower proportion of scale variation (~25-30%, similar or slightly higher than most Viverridae, Herpestidae and Hyaenidae).

Our results for magnitudes of integration are highly correlated to those for %isometry. Similarly to integration patterns, integration magnitudes show a structuring which also at least partially follows a taxonomic arrangement, with most felids highly integrated, *Nandinia* less integrated than some felids, but also presenting high values, *Prionodon* and *Hyaenas* showing low integration and Viverrids, Herpestids and

Euplerids having mostly low-to-intermediate values. Despite this overall structure, magnitudes of integration show considerable variation in all families with more than one well-estimated matrix, except for Hyaenidae which presents consistently low integration: the least integrated Feliforms are a herpestid (common dwarf mongoose, *Helogale parvula*) and a viverrid (banded palm civet, *Hemigalus derbyanus*), whereas another viverrid, *Paradoxurus musanga* (Asian palm civet), is as highly integrated as *Nandinia binotata* (African palm civet). As mentioned above for isometric variation three felids show remarkably low integration magnitudes, comparable to those for most viverrids and herpestids. Finally, as mentioned above, the cat-like fossa (*Cryptoprocta*, Eupleridae) is the second most integrated taxon examined, directly behind lions (*Panthera leo*). These findings for isometric variation and integration magnitudes have three important consequences. Firstly, the relatively structured variation of integration magnitudes in Feliformia does not necessarily contradict Porto *et al* (2009)'s statement that integration magnitudes show greater changes in relation to integration patterns in mammals; rather, the large variation seen in most families here may be seen as reason to lend further support to his conclusion. Secondly, the generally high integration seen among felids means that their limited shape diversity is likely at least in part influenced by within-population variational constraints, and not solely from a long-term history of selection aligned with a size dimension. Of course selection on size could also have played a role on felid diversification; an assessment of how much of a role it did play, and on which clades, would depend on an analysis directly dealing with the direction of selection pressures in the group, similarly to what Marroig & Cheverud (2010) did for neotropical primates. Finally, it is noticeable that the sometimes huge integration magnitude shifts occurring within Feliformia often coincide with convergences in morphology and in integration patterns.

In fact, our data show a surprising correlation between integration patterns, integration magnitudes and morphology (as well as size) within the suborder as a whole, even after correcting for effects of phylogenetic relatedness, as revealed by Mantel and partial Mantel Tests (Table 2-5). A correlation between integration patterns and morphology had been shown before for some groups of mammals (Oliveira *et al*, 2009; Costa, 2013; Rossoni, 2013), but not in others (Marroig & Cheverud, 2001; Hubbe, 2013), and may be interpreted as a sign that the evolution of inter-trait covariances is, at least to some degree, associated with the evolution of average trait values. One possible scenario that might cause this association is directional selection acting on population

means and concomitantly changing covariances. A possible alternative would be for covariance structures to be influenced by the average morphology simply due to the shape/form space underlying the set of variables used, as Rohlf (2000b) indicated for methods based on full trusses of 2-dimensional interlandmark distances with few landmarks (3 to at most 8). It is not at all clear, however, that this would also apply to sets of distances not representing the whole possible truss of distances between a larger number of landmarks. Moreover, the fact that a correlation between average morphology and integration patterns was not found in a clade with huge morphological disparities between species such as *Xenarthra* (Hubbe, 2013) testifies against relationships between average morphology and integration arising simply as a methodological artefact. Therefore, the correlation identified here between average morphology and integration patterns seems indeed to reflect associated evolution of trait means and covariances.

While correlations between average morphologies and integration patterns have already been noticed in some groups, as mentioned above, a coordination of changes in average morphological values and both patterns and magnitudes of integration had never been identified in previously studied mammalian groups, and might suggest that at least parts of Feliform diversification involved morphological evolution being accompanied by concerted evolution of both the orientation and the strength of character correlations. These concerted changes are found for Feliformia as a whole, and also among Feloidea (Felidae + Prionodontidae), the family Felidae, Herpestidae + Eupleridae, and in part within the subfamily Felinae (where integration magnitude is correlated to integration patterns, but not to morphology). It should be stressed that this association does not manifest as a simple straightforward correspondence of changes in average morphology and both aspects of integration. A combined examination of the distribution of taxa in the morphospace (**Appendix 8**) and in the integration pattern space (Fig. 1-4B), as well as of integration magnitude values (Fig 1-6A), shows that Felids, Hyaenids and Viverrids/Herpestids are more clearly separated in the morphospace than in integration patterns, and that the patterns for less integrated felids approximate those of the most integrated viverrids. In fact, while the first PCO axis of integration patterns (explaining 27.55% of total variance) is highly correlated to r^2 ($r = 0.86$; $p = 2.2 \cdot 10^{-16}$), a plot of integration patterns PCO1 against r^2 values shows that felids (and also Hyaeninae) have consistently higher PCO1 values in comparison to other taxa with similar r^2 values. Therefore, the situation seen for feliformians is not

that of a single, simple pattern/magnitude relationship. Rather, integration patterns are affected by the amount of integration, but also show other differences between groups, partly following morphological disparities (as evidenced by morphological convergences being sometimes mirrored by integration patterns).

Results of the Mantel test for identifying effects of phylogeny for Feliformia as a whole point to the existence of significant phylogenetic signal for all factors analysed but sociality (average morphology, magnitudes and patterns of morphological integration, as well as skull size and diet). The distance in integration patterns shows the highest correlation to phylogenetic distances of all factors analysed (0.431), once again indicating the relevance of the structuring of changes in integration patterns along the phylogeny. Results for phylogenetic signal using alternative methods (K/ Kmult), presented in **Appendix 16**, are mostly consistent with those of Mantel Tests in terms of the existence of significant phylogenetic signal in each factor, further corroborating the relevance of evolutionary history for changes in integration, as well as in diet, skull size and average morphology. It should be mentioned that the values of the K statistic are not directly comparable to those of Mantel correlations (Dutilleul *et al*, 2000; Blomberg *et al*, 2003); an in-depth analysis of the situations in interpretation of Mantel correlations and K values might make an interesting topic for future investigation.

Mantel tests within less inclusive clades show relations between integration patterns/magnitudes and the phylogeny occurring for most groups above the family level (Feloidea, Viverroidea, Hyaenidae + Eupleridae + Herpestidae), but never within families. Eupleridae might be the single exception, as correlations between phylogeny and patterns/ magnitudes within the family were high, although nonsignificant given the low species sample size for this group (n=5). This phylogenetic structuring partially agrees with, and complements the one previously seen for Feliformia by Goswami (2006a), who found an association between integration pattern similarity and phylogenetic distances within Feliformia (with branch lengths) and Felidae (using node-based distances). In addition to expanding the recognised effects of phylogeny on integration patterns to other clades within Feliformia, we also identify a formerly overlooked phylogenetic structure of the magnitudes of integration within the suborder. The association between the evolution of integration patterns and phylogenetic distances above, but not below the family level corroborates the structuration of covariation patterns seen in the integration space, and seems to indicate a constraint on integration patterns at the family level, beyond that which exists for mammals as a

whole (and possibly for Carnivora) due to generally shared developmental and functional patterns (Cheverud, 1996a; Marroig & Cheverud, 2001; Porto *et al.*, 2009).. This family-level constraint might, in fact, reflect functional or developmental particularities within general shared mammalian (and possibly carnivoran) arising from their shared evolutionary history. The analyses of relationships between character-specific evolutionary responses and phylogenetic distances show that phylogenetic effects are widespread in the skull for the suborder as a whole, with greater strength (based on Mantel correlations) in some characters at the oral region, two characters at the vault linked to the landmark PT (PT-BR, PT-EAM), and also a character related to the length of the top of the skull (NON-BR). Phylogenetic effects within the family Herpestidae (mongooses), on the other hand, are very weak and mostly non-significant.

Our results on the effects of evolutionary history on integration patterns, indicating differences structured at the family level, and changes not associated with the phylogeny within these groups, are once more akin to those observed for ruminants by Haber (2015). She found greater integration pattern diversification than expected under Brownian motion, taking this to imply that morphological integration may quickly respond to selection even if constrained at the family level. Haber argues that **P** matrix variation within phylogenetic groups, as seen for ruminants (and possibly for Feliformia, according to our results) would render the use of evolutionary analyses based on Lande (1979)'s equations problematic, since it would imply inconstancy of covariance patterns and a consequent difficulty in producing valid estimates of ancestral matrices. Although further investigation on the methods for ancestral matrix estimation is indeed an important point, we believe the similarity values found for most comparisons here (and arguably also in Haber, 2015) are still so high that pooled within-group covariance matrices remain very likely to represent reasonable, if not strictly true, representations of ancestral matrices, allowing the performance of evolutionary analyses.

The influence of diet on integration is perhaps the greatest difference between our results and those of Goswami (2006a). Her analysis, including 12 species of Feliformia, only three of which were not primarily carnivores, found no role for diet in the evolution of phenotypic integration within the suborder Feliformia. Including much wider taxonomic diversity and greater detail in diet characterisation (13 dietary classes against 4 in Goswami, 2006a; we also use a distance measure which considers dietary breadth), our work identifies dietary effects on integration pattern changes before

controlling for phylogenetic relatedness for Feliformia, and both before and after correction for phylogenetic relatedness in mongooses (Herpestidae). These results are found both with Mantel Tests and using alternative methods (D-PGLS - **Appendix 16**), lending further support to their validity. The correlation between diet and integration patterns only without phylogenetic correction, found for the suborder as a whole, may imply associated changes occurring along the evolutionary history of the group, but not within less inclusive phylogenetic groups. In other words, dietary changes are in fact part of the shared evolutionary history which shaped the differences in integration seen in Feliformia, as made clear from the high phylogenetic signal in integration. At least for Herpestidae, however, diet seems to exert pressures that directly influence and help shape character covariation patterns independently of phylogenetic relatedness, suggesting that, for mongooses at least, diet acts as a selective pressure acting on integration patterns. This might happen either directly, through directional selection for different functional and/or developmental integration, or indirectly, through selection on character means causing associated changes in morphological integration. The fact that average morphology is also highly correlated to diet in mongooses might suggest that the effects of diet on integration for this family are indirect, with diet acting as a selective pressure on average trait values and indirectly changing covariances. Alternative comparative methods, however, indicate average morphology as a good predictor of dietary habits, but not the opposite; also, diet is indicated as a good predictor of integration patterns, while average morphology is not (**Appendix 16**). If the directionality indicated for these relationships is correct, that might in fact indicate a direct effect of diet on trait covariances.

We also identified, for the first time to our knowledge, a relationship between diet and the magnitude of integration, found within the subfamily Felinae (small cats) both before and after correcting for phylogenetic distance. As all felids are primarily carnivores, diet variation among small cats relates mainly to preferential prey types (although the margay *Leopardus wiedii* also eats fruit - Konecny, 1989; Wang, 2002). Therefore, the link recognised between diet and magnitudes of integration may mean that some dietary items impose greater functional pressures, leading to higher integration in the skull or parts thereof. Alternatively, diet may be indirectly correlated to integration magnitudes through an association of diet with other life-history traits not measured in the present study, which in turn are related to size variation and therefore also to magnitudes of integration.

The analysis of dietary influences on character-specific selection response patterns (SRD) unsurprisingly shows strong effects of diet on characters at the oral region, for both Feliformia as a whole and Herpestidae. Interestingly, however, significant dietary influences are also found throughout the skull, including strong effects on some characters at the skull vault (e.g. BR-PT, PT-AS, LD-AS). It is in fact possible that such effects in characters at the vault might reflect functional aspects, as the temporal fossa, formed by the temporal and parietal bones, corresponds to the area of origin of the *temporalis* masticatory muscle (Done *et al*, 2009).

We found sociality to be related to size and average morphology in many groups, but not to integration in Feliformia as a whole and most of its subgroups, likely in part reflecting differences between usually larger group-hunters and mostly smaller taxa displaying cooperative territory protection and defence from predators, such as social mongooses. Additionally, the association between sociality and average morphology might also reflect changes in average skull morphology, mainly in the neurocranium, reflecting changes in the brain, as posed by the social brain hypothesis (Dunbar, 1998). Remarkably, we found a significant association between sociality and integration patterns within the family Herpestidae (mongooses). The persistence of an association between sociality and integration in this group according to the Mantel Tests even after correction for phylogenetic relatedness is remarkable, since sociality has a clear phylogenetic pattern within this family, with most social species grouped in one subfamily and most non-social taxa in another (Veron *et al*, 2004). Results using alternative comparative methods indicate sociality as a significant predictor of integration patterns only when not including phylogenetic covariances in the model, although variance in integration patterns in Herpestidae is better explained by sociality than by the split between subfamilies (D-PGLS, **Appendix 16**). Therefore, this result is also at least partly supported by both comparative methods used. As mentioned above for methods for recognising Phylogenetic Signal, an in-depth analysis dealing with the use of different comparative methods in studies of morphological integration would constitute an interesting future avenue for future investigation. .

Analysis of correlations between sociality and character-specific selection responses (SRD) shows a few significant effects for Feliformia as a whole, despite the lack of a general correlation with integration. These are found in the vault (PT-AS, PT-BR), as possibly expected according to the social brain hypothesis (Dunbar, 1998), but also within other regions, such as the zygomatic bone (ZS-ZI, ZI-ZYGI). Effects of

sociality within Herpestidae are both stronger and more widespread, including strong effects on the zygomatic arch and influences in various other facial characters. Part of these effects may possibly arise from some degree of correlation between diet and sociality within mongooses, as a correlation between these factors has indeed been recognised for this taxon, but these results also suggest more complex effects of sociality on integration than simply those related to expectations based on the social brain hypothesis. That notwithstanding, significant correlations between selection response patterns and social behaviour have indeed been found for various characters at the skull vault, lending support to the idea that sociality may not only affect average skull morphology along with changes in the brain, but also influence the evolution of integration patterns. As correlations between sociality and average morphology were also recognised in Herpestidae, this influence of sociality on integration patterns may arise from an indirect effect, through social pressures for increased (or differently shaped) brain size affecting average morphology and simultaneously altering covariance patterns. Also very interesting is the significant and very strong association of sociality with the selection response pattern of APET-BA, a character at the skull base which seems directly related to the degree of basicranial flexion, a trait previously shown to be related to spheroid skull (and brain) shapes and to relative brain size in primates (Gould, 1977; Ross & Ravosa, 1993; Ross & Henneberg, 1995; Lieberman *et al*, 2000). A previous study relating basicranial flexion and brain size in primates and some non-primate mammals unfortunately included only one non-social herpestid, *Galerella sanguinea* (Ross *et al*, 2004), and therefore is not of much use for comparative purposes within this group. Nevertheless, remarkable variation in basicranial flexion and skull roundness exists within the family: a rounded, spheroid-like skull is characteristic at least for the highly social meerkat (*Suricata suricatta* - van Staaden, 1994). A link between basicranial flexion and brain size within mongooses might therefore be a possible explanation for the high correlation between APET-BA selection responses and social behaviour, and this link between covariances involving basicranial flexion and brain size in carnivores constitutes a promising topic for future analyses. Previous work relating brain size to integration does exist for primates (Lieberman *et al*, 2000), but this is the first study to our knowledge to indicate a role of social behaviour in shaping skull phenotypic integration - especially outside primates. Our results thus highlight the possibility of ecological factors other than diet shaping integration, point to a

complexity of effects on integration possibly related to brain size changes and potentially other aspects.

One interesting point revealed by our analysis is the convergence in patterns and magnitudes of integration between two groups of "cat-like" hypercarnivores (*sensu* Van Valkenburgh, 2007). Felidae and the fossas (*Cryptoprocta*) shared very similar integration patterns, different from those of most other Feliformia, as well as remarkably high magnitudes of integration. The other hypercarnivore ecomorph present in extant Feliforms, bone-eating hyaenas (Hyaeninae), on the other hand, had a very low integration magnitude (shared with the remaining hyeanid *Proteles*), and a pattern of integration differing from those of both felids and viverrids/herpestids. This seems to indicate that patterns and magnitudes of integration have no single particular trend followed by all hypercarnivores. Still, the Felid-*Cryptoprocta* convergence not only in morphology, but also in integration patterns and magnitude might be indicative of a general tendency at least for cat-like hypercarnivores. The association of high integration, short snouts and large body size in *Cryptoprocta* and many felids is intriguing, and in fact is not particularly helpful for clarifying how these associated changes in morphology and integration may have come about in these groups. The high integration found in both cat-like groups is opposite to that found in *Homo* and *Gorilla*, for example, where short-faced morphologies with distinctive integration patterns are associated to a strong reduction of integration magnitude (Oliveira *et al*, 2009). Naturally, the factors leading to a shorter face in hominids and felids are very distinct: although it has been suggested that cats' shorter snouts may be associated to an increase in braincases along the lineage (Radinsky, 1982), this increase does not necessarily originate from a pressure for increased brain size as is usually supposed to happen for hominins at least (Wood & Collard, 1999; Zhang, 2003; Schroeder *et al*, 2014). Conversely, face reduction in cats is usually linked to hypercarnivory and its associated pressures for improved performance, which may have a bearing on cats' generally high magnitudes of integration and obviously did not happen in humans. A simple explanation for these differences linking integration to hypercarnivory-related functional pressures is precluded, however, by the fact that hyaenas do not show similarly high integration magnitudes, and also by the existence of at least three felids with low integration - the latter seeming to support Porto *et al* (2009) in that magnitudes are usually more labile than integration patterns.

Interestingly, the three less-integrated felids may be considered 'aberrant' representatives of the family in some way. *Panthera uncia* is well-known for its disparity in relation to other pantherines (Hemmer, 1966; Mazák, 1983; Werdelin, 1983), with a particularly short rostrum more closely approximating large members of the small-cat lineage like *Acinonyx jubatus* and *Puma concolor* (Christiansen, 2008a; Sicuro, 2011; Sicuro & Oliveira, 2011; Sakamoto & Ruta, 2012). *Leopardus tigrinus* and its recently describe sister species *Leopardus guttulus* and *Leopardus wiedii* may be less distinctive from other *Leopardus*, but also show remarkable particularities in skull shape. The skulls of *L. tigrinus/guttulus* and also *L. wiedii* all have a convex shape in the region of the frontal bone (Nascimento, 2010), and their skull shape is considered similar in a number of aspects by Sakamoto & Ruta (2012) and Sicuro & Oliveira (2011). *L. tigrinus* also has the most narrow, delicate zygomatic arch among *Leopardus* species (Sicuro & Oliveira, 2011), as well as non-projected anterior premaxillar extremity, giving the skull an even shorter snout and a "flat" profile in lateral view (Nascimento, 2010). All instances of low integration in felids are thus associated with particular changes in morphology. *L. wiedii* in particular is the only fruit-eating cat, so for this species dietary changes may also play a role in its lower integration.

Asian linsangs (*Prionodon*) are not usually considered "typical" hypercarnivores, but their dentition has been considered hypercarnivorous by Wozencraft (1984), which is at least partially corroborated by current knowledge about its diet (Davis, 1958; Lim, 1973; Pham-Chong-Ahn, 1980). If they in fact do represent a further hypercarnivorous clade, they would represent a completely different ecomorph, convergent with *Poiana* (which is not strictly carnivorous) in morphology, but not in integration patterns, with *Poiana* seemingly close to viverrids and *Prionodon* showing a pattern somewhat different from that of other families, as mentioned above, and displaying low integration magnitude (for *Prionodon* at least).

The consistency in morphology and phenotypic integration among bone-cracking hyaenas and among cats and cat-like *Cryptoprocta*, but not between these groups, suggests as a further future avenue of study a detailed comparison of morphology, diet and integration (whenever possible) in various lineages of traditionally recognised hypercarnivore ecomorphs ("wolf-like", "hyaena-like" and "cat-like" - Van Valkenburgh, 2007) and closely related groups, including possibly different hypercarnivores like *Prionodon*, as well as fossil lineages. Studies of phenotypic integration in fossils are remarkably difficult because of the great difficulty in obtaining

representative samples for characterisation of the covariance structure. Nevertheless, some such studies do exist at least for Machairodontinae felids (*Smilodon* - Goswami, 2006b; Goswami *et al*, 2014), Nimravids (*Dinictis* and *Hoplophoneus* - Goswami, 2006b) and the dog-like hyaenids *Thalassictis* (Goswami, 2006b; see Turner *et al*, 2008), as well as the caniforms *Canis dirus*, *Hesperocyon* (Canidae - Goswami 2006b) and *Daphoenus* (Amphicyonidae). Although covariance matrices have been estimated using relatively low sample sizes in some of these works, which might cast doubts on their representativeness, analyses using relatively lower dimensionality might in fact allow interesting insights on the phenotypic integration of at least some fossil taxa.

One possible limitation of our study is the lack of an estimated **G** matrix within not only Carnivores, but Laurasiatheria as a whole, which might be argued to undermine inferences regarding the evolutionary significance of the morphological integration changes seen here. However, not only has it been argued that the **P** matrix is evolutionary meaningful on its own right (Burger, 1986; Steppan, 1997a; Pitchers *et al*, 2013), but great **G-P** similarity also tends to hold, to a considerable degree, within mammals as a whole for skull morphology (Porto *et al*, 2009). Porto *et al* (2009)'s study specifically showed remarkable similarity between the **P** matrix of a carnivore, *Cerdocyon*, and the **G** matrix of a distantly related rodent (*Akodon cursor*), suggesting that **P** matrices may in fact represent reasonable estimates of **G** for carnivores. This, of course, does not lessen the value of future works directly estimating **G** matrices for Laurasiatherians, Carnivores and Feliformians. Promising methods to do so might involve the use of genealogies of domesticated animals such as cats (*Felis catus*), studbooks of zoo specimens (i.e. Müller, 2012) with material preserved in collections, or even skulls from groups of social species under long-time monitoring (e.g. the Kalahari Meerkat Project, www.kalahari-meerkats.com).

Our study thus shows high similarity, but also a remarkable structuring of phenotypic integration patterns among different families and/or groups of feliform Carnivora (felids; hyaenids; viverrids/euplerids; Prionodontidae), with a general association not only between average morphology and integration patterns, but also between these and integration magnitudes, within the group as a whole and some subgroups (ex. Felidae). Influences of phylogeny on integration patterns were found for the majority of more inclusive phylogenetic groups, but never within families, indicating the existence of differences expressed mostly at the family level in the generally highly conserved covariance structure within Feliformia. Variation in

integration patterns within families, on the other hand, seems to be further constrained by the general family pattern, although integration differences related to ecological factors do occur in at least one family.. Unlike a previous analysis of integration in Carnivora (Goswami, 2006a), we found diet to diversify together with integration patterns along the phylogeny of Feliformia, and show that dietary changes act as drivers of the evolution of integration patterns (in mongooses) and magnitudes (in small cats) in parts of this suborder. We show that sociality is mainly related to body size and skull morphology in feliforms - possibly partly reflecting selective pressures on brain size and/or shape in social taxa. We also show, however, that social behaviour does influence integration patterns at least among mongooses (Herpestidae), pointing to putative links between integration, brain growth and possibly other factors in this family, which may constitute an interesting direction for future studies. Given the presence of a pattern-magnitude relationship differing among families, the different sets of factors influencing integration in each subgroup, and also the existence of interesting convergences in integration following morphological convergences in some, but possibly not all groups, this work suggests a complex interaction of factors affecting skull morphological integration in feliforms and opens up interesting new directions of study to help better understand the links between evolutionary changes in average morphology, integration and ecology in this fascinating group.

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References

- Abdi, H. 2007. The RV coefficient and the congruence coefficient. *In*: Salkind, N. (ed). Encyclopedia of Measurement and Statistics, Sage, Thousand Oaks, CA.
- Adams, D.C. 2014a. A generalized K statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data. *Systematic Biology* 63(5): 685-697.
- Adams, D.C. 2014b. A method for assessing phylogenetic least squares models for shape and other high-dimensional multivariate data. *Evolution* 68(9): 2675-2688.
- Adams, D.C.; Rohlf, F.J.; Slice, D.E. 2004. Geometric morphometrics: ten years of progress following the 'revolution'. *Italian Journal of Zoology* 71: 5-16.
- Armbruster, W.S.; Pélabon, C.; Bolstad, G.H.; Hansen, T.F. 2014. Integrated phenotypes: understanding trait covariation in plants and animals. *Philosophical Transactions of the Royal Society B: Biological Sciences* 369 (1649): doi: 10.1098/rstb.2013.0245.
- Arnold, J.A.; Pfrender, M.E.; Jones, A.G. 2001. The adaptive landscape as a conceptual bridge between micro- and macroevolution.
- Arnold, S.J.; Burger, R.; Hohenlohe, P.A.; Ajie, B.C.; Jones, A.G. 2008. Understanding the evolution and stability of the G-matrix. *Evolution* 62(10): 2451-2461.
- Arnold, S.J.; Phillips, P.C. 1999. Hierarchical comparison of genetic variance-covariance matrices. II. Coastal-inland divergence in the garter snake, *Thamnophis elegans*. *Evolution* 53(5): 1516-1527.
- Bailey, I.; Myatt, J.P.; Wilson, A.M. 2013. Group hunting within the Carnivora: physiological, cognitive and environmental influences on strategy and cooperation. *Behavioural Ecology and Sociobiology* 67:1-17.
- Barycka, E. 2007. Evolution and systematics of the feliform Carnivora. *Mammalian Biology* 72(5):157-282.
- Björklund, M.; Husby, A.; Gustafsson, L. 2012. Rapid and unpredictable changes of the G-matrix in a natural bird population over 25 years. *Journal of Evolutionary Biology* 26: 1-13.
- Blomberg, S.P.; Garland T.; Ives, A.R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57(4): 717-745.
- Bolstad, G.H.; Hansen, T.F.; Pélabon, C.; Falahati-Anbara, M.; Pérez-Barrales, R.; Armbruster, W.C. 2014. Genetic constraints predict evolutionary divergence in *Dalechampia* blossoms. *Philosophical Transactions of the Royal Society B* 369: DOI: 10.1098/rstb.2013.0255
- Bookstein, F.L. 1996. Biometrics, biomathematics and the morphometric synthesis. *Bulletin of Mathematical Biology* 58: 313-365.
- Burger, R. 1986. Constraints for the evolution of functionally coupled characters: A nonlinear analysis of a phenotypic model. *Evolution* 40(1): 182-193.
- Burt, C. 1984. Factor analysis and canonical correlations. *British Journal of Psychology, Statistical Section* 1: 95-106.
- Cheverud, J.M. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. *Evolution* 36(3): 499-516.
- Cheverud, J.M. 1984. Quantitative genetics and developmental constraints on evolution by selection. *Journal of Theoretical Biology* 110 (2): 155-171.
- Cheverud, J.M. 1988. A comparison of genetic and phenotypic correlations. *Evolution* 42: 958-968
- Cheverud, J.M. 1995. Morphological Integration in the Saddle-Back Tamarin (*Saguinus fuscicollis*) Cranium. *The American Naturalist* 145(1): 63-89.
- Cheverud, J.M. 1996a. Quantitative genetic analysis of cranial morphology in the cotton-top (*Saguinus oedipus*) and saddle-back (*Saguinus fuscicollis*) tamarins.
- Cheverud, J.M. 1996b. Developmental Integration and the Evolution of Pleiotropy. *American Zoologist* 36: 44-50.
- Cheverud, J.M.; Marroig, G. 2007. Comparing covariance matrices: random skewers method compared to the common principal components model. *Genetics and Molecular Biology* 30(2): 461-469.
- Christiansen, P. 2008a. Evolutionary changes in craniomandibular shape in the great cats (*Neofelis* Griffith and *Panthera* Oken). *Biological Journal of the Linnean Society* 95: 766-778.
- Christiansen, P. 2008b. Evolution of skull and mandible shape in cats (Carnivora: Felidae). *PLoS ONE* 3 (7): e2807
- Christiansen, P. 2008c. Species distinction and evolutionary differences in the Clouded Leopard (*Neofelis nebulosa*) and Diard's Clouded Leopard (*Neofelis diardi*). *Journal of Mammalogy* 89(6): 1435-1446.

- Claude, J.; Jolliffe, I.T.; Zuur, A. 2007. Multivariate analyses of morphometric turtle data - size and shape. *In*: Zuur, A.; Ieno, E.N.; Smith, G.M. (eds). *Analysing Ecological Data*. Springer. pp 529-546.
- Costa, B.M.A. 2013. Evolução e integração morfológica do crânio dos roedores da subfamília Sigmodontinae Wagner, 1843 (Rodentia, Cricetidae). Doctoral dissertation, Universidade de São Paulo.
- Darwin, C. 1859. *On the Origin of Species by Natural Selection*. London: J. Murray.
- Davis, D.D. 1958. Mammals of the Kelabit Plateau, northern Sarawak. *Fieldiana Zoology* 39: 119-147.
- Done, S.H.; Goody, P.C.; Evans, S.A.; Stickland, N.C. 2009. *Color Atlas of Veterinary Anatomy, Volume 3: The Dog and Cat*. Elsevier Health Sciences.
- Drake, A.B.; Klingenberg, C.P. 2010. Large-Scale Diversification of Skull Shape in Domestic Dogs: Disparity and Modularity. *The American Naturalist* 175(3): 289-301.
- Driscoll, C.A.; Menotti-Raymond, M.; Roca, A.L.; Hupe, K.; Johnston, W.E.; Geffen, E.; Harley, E.H.; Delibes, M.; Pontier, D.; Kitchener, A.C.; Yamaguchi, N.; O'Brien, S.J.; Macdonald, D.W. 2007. The Near Eastern Origin of Cat Domestication. *Science* 317: 519-523.
- Dryden, I.L.; Mardia, K.V. 1998. *Statistical shape analysis*. John Wiley & Sons, New York.
- Dunbar, R.M. 1998. The social brain hypothesis. *Evolutionary Anthropology* 7: 178-190.
- Dutilleul, P.; Stockwell, J.D.; Frigon, D.; Legendre, P. 2000. The Mantel Test versus Pearson's correlation analysis: assessment of the differences for biological and environmental studies. *Journal of Agricultural, Biological and Environmental Statistics* 5(2): 131-150.
- Felsenstein, J. 1988. Phylogenies and quantitative characters. *Annual Review of Ecology, Evolution and Systematics* 19: 445-471.
- Finarelli, J.A.; Flynn, J.J. 2009. Brain-size evolution and sociality in Carnivora. *PNAS* 106(23): 9345-9349.
- Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Oxford University Press.
- Freckleton, R.P.; Harvey, P.H.; Pagel, M. 2002. Phylogenetic Analysis and Comparative Data: A Test and Review of Evidence. *The American Naturalist* 160(6): 712-726.
- Frontier, S. 1976. Étude de la décroissance des valeurs propres dans une analyse en composantes principales: comparaison avec le modèle de baton brisé. *Journal of Experimental Marine Biology and Ecology* 25: 67-75.
- Garcia, G.; Hingst-Zaher, E.; Cerqueira, R.; Marroig, G. 2014. Quantitative Genetics and Modularity in Cranial and Mandibular Morphology of *Calomys expulsus*. *Evolutionary Biology* 41(4): 619-636.
- Gilchist, J.S.; Jennings, A.P. Veron, G.; Cavallini, P. 2009. Family Herpestidae (Mongooses) *In*: *Handbook of the Mammals of the World. Volume 1: Carnivores*. Wilson, D.E.; Mittermeier, R.A. (orgs) Lynx Edicions, 2009.
- Goldman, C.A. 1987. *Crossarchus obscurus*. *Mammalian Species* 290:-1.5
- González-José, R.; Van der Molen, S.; González-Pérez, E.; Hernández, M. 2004. Patterns of Phenotypic Covariation and Correlation in Modern Humans as Viewed from Morphological Integration. *American Journal of Physical Anthropology* 123:69-77.
- Goswami, A. 2006a. Morphological integration in the carnivoran skull. *Evolution* 60 (1): 169-183.
- Goswami, A. 2006b. Cranial Modularity Shifts during Mammalian Evolution. *The American Naturalist* 168(2): 270-280.
- Goswami, A.; Milne, N.; Wroe, S. 2011. Biting through constraints: cranial morphology, disparity and convergence across living and fossil carnivorous mammals. *Proceedings of the Royal Society B: Biological Sciences* 278: 1831-1839. doi: 10.1098/rspb.2010.2031
- Goswami, A.; Polly, P.D. 2010a. The Influence of Modularity on Cranial Morphological Disparity in Carnivora and Primates (Mammalia). *PLoS ONE* 5(3): e9517.
- Goswami, A.; Polly, P.D. 2010a. The influence of modularity on cranial morphological disparity in Carnivora and Primates (Mammalia). *PloS One* 5(3).
- Goswami, A.; Polly, P.D. 2010b. Methods for studying morphological integration and modularity. *In*: Alroy, J; Hunt, E.G. (eds). *Quantitative Methods in Paleobiology*. Paleontological Society Papers 16: 213-243.
- Goswami, A.; Smaers, J.B.; Soligo, C.; Polly, P.D. 2014. The macroevolutionary consequences of phenotypic integration: from development to deep time. *Philosophical transactions of the Royal Society B* 369: doi: 10.1098/rstb.2013.0254.
- Gould, S.J. 1977. *Ontogeny and Phylogeny*. Cambridge: Belknap Press.
- Gould, S.J.; Lewontin, R.C. 1979. The Spandrels of San Marco and the Panglossian Paradigm: a Critique of the Adaptationist Programme.

- Proceedings of the Royal Society of London B: Biological Sciences 205(1161): 581-598.
- Gower, J.C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *biometrika* 53(3/4): 325-338.
- Gower, J.C. 1971. A General Coefficient of Similarity and Some of its Properties. *Biometrics* 27(4): 857-871.
- Gross, J.B.; Hanken, J. 2008. review of fate-mapping studies of osteogenic cranial neural crest in vertebrates. *Developmental Biology* 317: 389-400.
- Guillot, G.; Rousset, F. 2013. Dismantling the Mantel tests. *Methods in Ecology and Evolution* 4: 336-344.
- Haber, A. 2015. The Evolution of Morphological Integration in the Ruminant Skull. *Evolutionary Biology* 42: 99-114.
- Hallgrímsson, B.; Jamniczky, H.; Young, N.; Rolian, C.; Parsons, T.; Boughner, J.; Marcucio, R. 2009. Deciphering the palimpsest: studying the relationship between morphological integration and phenotypic covariation. *Evolutionary Biology* 36(4): 355-376.
- Hallgrímsson, B.; Lieberman, D.E.; Young, N.M.; Parsons, T.; Wat, S. 2007. Evolution of covariance in the mammalian skull. *In: Tinkering: the microevolution of development*. Novartis Foundation Symposium 284. Chichester: Wiley.
- Hallgrímsson, B.; Willmore, K.; Hall, B.K. 2002. Canalization, developmental stability, and morphological integration in primate limbs. *Yearbook of Physical Anthropology* 45: 131-158.
- Hansen, T.; Houle, D. 2008. Measuring and comparing evolvability and constraint in multivariate characters. *Journal of Evolutionary Biology*, 21(5): 1201-1219.
- Harmon, L.J.; Glor, R.E. 2010. Poor statistical performance of the Mantel Test in phylogenetic comparative analyses. *Evolution* 64(7): 2173-2178.
- Hemmer, H. 1966. Untersuchungen zur Stammesgeschichte der Pantherkatzen (Pantherinae). Teil I. Veröffentlichungen der zoologischen Staatssammlung München 11:1-121.
- Holekamp, K.E.; Dantzer, B.; Stricker, G.; Yoshida, K.C.S.; Benson-Amram, S. 2015. Brains, brawns and sociality: a hyaena's tale. *Animal Behaviour* 103: 237-248.
- Hotelling, H. 1936. Relations between two sets of variates. *Biometrika* 28: 321.
- Hubbe, A. 2013. Análise morfológica craniana de *Xenarthra* atuais e extintos: inferências evolutivas e funcionais. Doctoral dissertation, Universidade de São Paulo.
- IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. Available at www.iucnredlist.org.
- Jolicoeur, P. 1963. The Multivariate Generalization of the Allometry Equation. *Biometrics* 19: 497-499.
- Jolicoeur, P.; Mosimann, J.E. 1960. Size and shape variation in the painted turtle. A principal component analysis. *Growth* 24: 339-354.
- Jones, A.G.; Arnold, S.J.; Burger, R. 2003. Stability of the G-matrix in a population experiencing pleiotropic mutation, stabilizing selection, and genetic drift. *Evolution* 57(8): 1747-1760.
- Jones, A.G.; Arnold, S.J.; Burger, R. 2004. Evolution and stability of the G-matrix on a landscape with a moving optimum. *Evolution* 58(8): 1639-1654.
- Jones, A.G.; Arnold, S.J.; Bürger, R. 2007. The Mutation Matrix and the Evolution of Evolvability. *Evolution* 61(4): 727-745.
- Jones, A.G.; Burger, R.; Arnold, S.J.; Hohenlohe, P.A.; Uyeda, J.C. 2012. The effects of stochastic and episodic movement of the optimum on the evolution of the G-matrix and the response of the trait mean to selection. *Journal of Evolutionary Biology* 25(11): 2210-2231.
- Kingdom, J.; Hoffman, M. 2013. The Mammals of Africa V: Carnivores, Pangolins, Equids and Rhinoceroses. Bloomsbury, London, UK. pp. 328-330.
- Kissling, W.D.; Dalby, L.; Fløjgaard, C.; Lenoir, J.; Sandel, B.; Sandom, C.; Trøjsgaard, K.; Svenning, J.-S. 2014. Establishing macroecological trait datasets: digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecology and Evolution* 4(14): 2913-2930.
- Kitchener, A.C.; Van Valkenburgh, B.; Yamaguchi, N. 2010. Felid form and function. *In: MacDonald, D.W.; Loveridge, A.J. (eds). Biology and Conservation of Wild Felids*. pp. 83-106. Oxford: Oxford University Press.
- Klingenberg, C. 2008. Morphological integration and developmental modularity. *Annual Review of Ecology, Evolution and Systematics* 39: 115-132.
- Klingenberg, C.P. 2009. Morphometric integration and modularity in configurations of landmarks: tools for evaluating a priori hypotheses. *Evolution and Development* 11(4): 405-421.
- Klingenberg, C.P. 2013. Cranial integration and modularity: insights into evolution and

- development from morphometric data. *Hystrix, the Italian Journal of Mammalogy* 24(1): 43-58.
- Klingenberg, C.P. 2014. Studying morphological integration and modularity at multiple levels: concepts and analysis. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 369 (1649) doi: 10.1098/rstb.2013.0249
- Klingenberg, C.P.; Zaklan, S.D. 2000. Morphological integration between developmental compartments in the *Drosophila* wing. *Evolution* 54: 1273-1285.
- Konecny, M.J. 1989. Movement patterns and food habits of four sympatric carnivores species in Belize, Central America. In: Redford, K.H.; Eisenberg, J.F. (eds). *Advances in Neotropical Mammalogy*, pp 243-264. Sandhill Crane Press, Gainesville, Florida.
- Koyabu, D.; Werneburg, I.; Morimoto, N.; Zollikofer, C.P.E.; Forasiepi, A.M.; Endo, H.; Kimura, J.; Ohdachi, S.D.; Truong Son, N.; Sánchez-Villagra, M.R. 2013. Mammalian skull heterochrony reveals modular evolution and a link between cranial development and brain size. *Nature Communications* 5: 3625. doi: 10.1038/ncomms4625
- Krzanowski, W.J. 1979. Between-Groups Comparison of Principal Components. *Journal of the American Statistical Association* 74(367): 703.
- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution* 33(1): 402-416.
- Lande, R. 1986. The dynamics of peak shifts and the pattern of morphological evolution. *Paleobiology* 12: 343-354.
- Lande, R.; Arnold, S.J. 1983. The measurement of selection on correlated characters. *Evolution* 37: 1210-1226.
- Lapointe, F.J.; Garland, T. 2001. A generalized permutation model for the analysis of cross-species data. *Journal of Classification* 18: 109-127.
- Lele, S.; Cole, T.M.III. 1996. A new test for shape differences when variance-covariance matrices are unequal. *Journal of Human Evolution* 31: 193-212.
- Lele, S.; Richtsmeier, J.T. 1991. Euclidean distance matrix analysis: a coordinate free approach for comparing biological shapes using landmark data. *American Journal of Physical Anthropology* 86: 415-427.
- Lessels, C.M.; Boag, P.T. 1987. Unrepeatable repeatabilities: A common mistake. *The Auk* 104: 116-121.
- Li, G.; Davis, B.W.; Eizirik, E.; Murphy, W.J. 2016. Phylogenomic evidence for ancient hybridization in the genomes of living cats (Felidae). *Genome Research* 26(1): 1-11. doi: 10.1101/gr.186668.114.
- Liebermann, D.E.; Ross, C.F.; Ravosa, M.J. 2000. The primate cranial base: Ontogeny, function and integration. *Yearbook of Physical Anthropology* 43: 117-169.
- Lim, B.L. 1973. The banded linsang and the banded musang of West Malaysia. *Malayan Natural History Journal* 26: 105-111.
- van der Linde, K.; Houle, D. 2009. Inferring the Nature of Allometry from Geometric Data. *Evolutionary Biology* 36: 311-322.
- Linde-Medina, M.; Boughner, J.C.; Santana, S.E.; Diogo, R. 2016. Are more diverse parts of the mammalian skull more labile? *Ecology and Evolution*. doi:10.1002/ece3.2046.
- Macdonald, D.W.; Yamaguchi, N.; Kerby, G. 2000. Group-living in the domestic cat: its sociobiology and epidemiology. In: *The Domestic Cat: The Biology of Its Behaviour*. Turner, D.C. Cambridge University Press. pp 95-118.
- Marroig, G.; Cheverud J.M.. 2001. A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology, and ontogeny during cranial evolution of new world monkeys. *Evolution* 55(12): 2576-600.
- Marroig, G.; Cheverud J.M.. 2005 Size as a line of least evolutionary resistance: diet and adaptive morphological radiation in New World monkeys. *Evolution* 59(5): 1128-42
- Marroig, G.; Cheverud, J.M. 2010. Size as a line of least resistance II: direct selection on size or correlated response due to constraints? *Evolution* 64: 1470-1488.
- Marroig, G.; Melo, D.; Porto, A.; Sebastião, H.; Garcia, G. 2011. Selection Response Decomposition (SRD): A New Tool for Dissecting Differences and Similarities Between Matrices. *Evolutionary Biology* 38: 225-241.
- Marroig, G.; Shirai, L.T.; Porto, A.; Oliveira, F.B.; Conto, V. 2009. The evolution of modularity in the mammalian skull II: Evolutionary consequences. *Evolutionary Biology* 36(1): 136-148
- Martin, L.D. 1989. Fossil history of terrestrial carnivora. In: Gittleman, J.L. ed. *Carnivore behaviour, ecology, and evolution*. New York, NY: Cornell University Press: 536-568.
- Martínez-Abadías, N.; Esparza, M.; Sjøvold, T.; González-José, R.; Santos, M.; Hernández, M.; Klingenberg, C.P. 2011. Pervasive Genetic Integration Directs the Evolution of Human Skull Shape. *Evolution* 66(4): 1010-1023

- Mattern, M.Y.; McLennan, D.A. 2000. Phylogeny and Speciation of Felids. *Cladistics* 16(2): 232-253.
- Mazák, V. 1983. *Der Tiger*. Wittenberg Lutherstadt: Neue Brehm-Bücherei 356, A. Ziemsen Verlag.
- Melo, D.; Garcia, G.; Hubbe, A. Assis, A.P.; Marroig, G. 2015. *EvolQG* - An R package for evolutionary quantitative genetics [version 1; referees:1 approved, 1 approved with reservations] F1000Research 4:925.
- Meloro, C.; Slater, G.J. 2012. Covariation in the Skull Modules of Cats: the Challenge of growing Saber-like Canines. *Journal of Vertebrate Paleontology* 32(3): 677-685.
- Monteiro, L.R.; Bonato, V.; Dos Reis, S.F. 2005. Evolutionary integration and morphological diversification in complex morphological structures: Mandible shape divergence in spiny rats (Rodentia, Echimyidae). *Evolution and Development* 7 (5): 429-439.
- Monteiro, L.R.; Nogueira, M.R. 2009. Adaptive radiations, ecological specialization and the evolutionary integration of complex morphological structures. *Evolution* 64(3): 724-744.
- Moore, W.J. 1981. *The mammalian skull*. Cambridge: Cambridge University Press.
- Mosimann, J.E. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. *Journal of the American Statistical Association* 65: 930-945.
- Müller, P. 2012. General register, Bengal Tigers *Panthera tigris tigris* (Linné, 1758) registered until December 15, 2012. Available at: <http://cza.nic.in/International%20Studbook%20of%20Bengal%20Tiger.pdf>. Accessed in April 2nd, 2016.
- Nascimento, F.O. 2010. Revisão taxonômica do gênero *Leopardus* Gray, 1842 (Carnivora, Felidae). Doctoral dissertation, Instituto de Biociências, Universidade de São Paulo.
- Nei, M. 2013. *Mutation-Driven Evolution*. Oxford: Oxford University Press.
- Noonan, M.J.; Newman, C.; Buesching, C.D.; Macdonald, D.W. 2015. Evolution and function of fossoriality in the Carnivora: implications for group-living. *Frontiers in Ecology and Evolution* 3: 116. doi: 10.3389/fevo.2015.00116.
- Nyakatura, K.; Bininda-Emonds, O.R.P. 2012. Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. *BMC Biology* 10(12): doi:10.1186/1741-7007-10-12
- Oliveira, F.B.; Porto, A.; Marroig, G. 2009. Covariance structure in the skull of Catarrhini: a case of pattern stasis and magnitude evolution. *Journal of Human Evolution* 56(4): 417-430.
- Olson, E.V.; Miller, R.L. 1951. A mathematical model applied to a study of the evolution of species. *Evolution* 5(4): 325-338
- Olson, E.V.; Miller, R.L. 1958. *Morphological Integration*. Chicago: University of Chicago Press
- Patou, M.-L.; Mclenachan, P.A.; Morley, C.G.; Couloux, A.; Jennings, A.P.; Veron, G. 2009. Molecular phylogeny of the Herpestidae (Mammalia, Carnivora) with a special emphasis on the Asian *Herpestes*. *Molecular Phylogenetics and Evolution* 53: 69-80.
- Pavlicev, M.; Wagner, G.; Cheverud, J.M. 2009a. Measuring evolutionary constraints through the dimensionality of the phenotype: Adjusted bootstrap method to estimate rank of phenotypic covariance matrices. *Evolutionary Biology* 36(3): 339-353.
- Phang-Chong-Ahn. 1980. A contribution to the morphology and ecology of the Viverridae (Mammalia) in Vietnam. *Zoologicheskii zhurnal* 59: 905-914.
- Phillips, P.C.; Whitlock, M.C.; Fowler, K. 2001. Inbreeding changes the shape of the genetic covariance matrix in *Drosophila melanogaster*. *Genetics* 158(3): 1137-1145.
- Pitchers, W.R.; Brooks, R.; Jennions, M.D.; Tregenza, T.; Dworkin, I.; Hunt, J. 2013. Limited plasticity in the phenotypic variance-covariance matrix for male advertisement calls in the black field cricket, *Teleogryllus commodus*. *Journal of Evolutionary Biology* 26(5): 1060-1078.
- Porto, A.; Oliveira, F.B.; Shirai, L.T.; de Conto, V.; Marroig, G. 2009. The Evolution of Modularity in the Mammalian Skull I: Morphological Integration Patterns and Magnitudes. *Evolutionary Biology* 36:118-135.
- Porto, A.; Shirai, L.T.; Oliveira, F.B.; Marroig, G. 2013. Size variation, growth strategies and the evolution of modularity in the mammalian skull. *Evolution* 67(11): 3305-3322
- R Core Team 2015. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Radinsky, L.B. 1982. Evolution of skull shape in carnivores. 3. The origin and early radiation of the modern carnivore families. *Paleobiology* 8: 177-195.
- Rao, C.R.; Suryawanshi, S. 1996. Statistical analysis of shape of objects based on landmark data. *Proceedings of the National Academy of Sciences of the U.S.A.* 93: 12132-12136.

- Rapson, S.A.; Goldizen, A.W.; Seddon, J.M. 2012. Species boundaries and possible hybridization between the black mongoose (*Galerella nigrata*) and the slender mongoose (*Galerella sanguinea*). *Molecular Phylogenetics and Evolution* 65: 831-839.
- Reusch, T.; Blanckenhorn, W.U. 1998. Quantitative genetics of the dung fly *Sepsis cynipsea*: Cheverud's conjecture revisited. *Heredity* 81: 111-119.
- Revell, L.J. 2007. The G matrix under fluctuating correlational mutation and selection. *Evolution* 61(8): 1857-1872.
- Revell, L.J. 2010. Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution* 1: 319-329.
- Revell, L.J. 2012. phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3: 217-223. doi:10.1111/j.2041-210X.2011.00169.x
- Richtsmeier, J.T.; Flaherty, K. 2013. Hand in glove: brain and skull in development and dysmorphogenesis. *Acta Neuropathologica* 125: 1-21.
- Roff, D.A. 1995. The estimation of genetic correlations from phenotypic correlations: a test of Cheverud's conjecture. *Heredity* 74: 481-490.
- Roff, D.A. 2000. The evolution of the G matrix: Selection or drift? *Heredity* 84(2): 135-142.
- Roff, D.A.; Mousseau, T. 2005. The evolution of the phenotypic covariance matrix: Evidence for selection and drift in *Melanoplus*. *Journal of Evolutionary Biology* 18(4): 1104-1114.
- Rohlf, F.J. 2000a. Statistical power comparisons among alternative morphometric methods. *American Journal of Physical Anthropology* 111(4): 463-478.
- Rohlf, F.J. 2000b. On the use of shape spaces to compare morphometric methods. *Hystrix* 11: 9-25.
- Rohlf, F.J. 2003. Bias and error in estimates of mean shape in geometric morphometrics. *Journal of Human Evolution* 44: 665-683.
- Rohlf, F.J.; Marcus, L.F. 1993. A revolution in morphometrics. *Trends in Ecology and Evolution* 8: 129-132.
- Rohlf, F.J.; Slice, D.E. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* 39: 40-59.
- Ross, C.F.; Henneberg, M. 1995. Basicranial flexion, relative brain size and facial kyphosis in *Homo sapiens* and some fossil hominids. *American Journal of Physical Anthropology* 98: 575-593.
- Ross, C.F.; Henneberg, M.; Ravosa, M.J.; Richard, S. 2004. Curvilinear, geometric and phylogenetic modeling of basicranial flexion: is it adaptive, is it constrained? *Journal of Human Evolution* 46: 185-213.
- Ross, C.F.; Ravosa, M. 1993. Basicranial flexion, relative brain size and facial kyphosis in nonhuman primates. *American Journal of Physical Anthropology* 91: 305-324.
- Rossoni, D.M. 2013. Integração morfológica craniana em morcegos da Família Phyllostomidae. Doctoral dissertation, Universidade de São Paulo.
- Ruiz-Garcia, M.; Corrales, C.; Pinedo-Castro, M. 2012. Craniometric and Microsatellite genetic differentiation among putative ocelot subspecies (*Leopardus pardalis*) throughout Latin America. In: *Molecular Population Genetics, Phylogenetics, Evolutionary Biology and Conservation of the Neotropical Carnivores*. Ruiz-Garcia, M.; Shostell, J. (eds). Nova Science Publishers, Inc., New York (USA).
- Sakamoto, M.; Ruta, M. 2012. Convergence and Divergence in the Evolution of Cat Skulls: Temporal and Spatial Patterns of Morphological Diverity. *PLoS ONE* 7(7): e39752.
- Schluter, D. 1996. Adaptive Radiation along Genetic Lines of Least Resistance. *Evolution* 50(5): 1766-1774.
- Schroeder, L.; Roseman, C.C.; Cheverud, J.M.; Ackermann, R.R. 2014. Characterizing the Evolutionary Path(s) to Early Homo. *PLoS ONE* 9(12): e114307
- Schultz, S.; Dunbar, R. 2010. Encephalization is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. *PNAS* 107(50): doi: 10.1073/pnas.100524107.
- Shirai, L.T.; Marroig, G. 2010. Skull modularity in neotropical marsupials and monkeys: size variation and evolutionary constraint and flexibility. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 314B(8): 663-683
- Sicuro, F.L. 2011. Evolutionary trends on extant cat skull morphology (Carnivora: Felidae): a three-dimensional geometrical approach. *Biological Journal of the Linnean Society* 103: 176-190.
- Sicuro, F.L.; Oliveira, L.F.B. 2011. Skull morphology and functionality of extant Felidae (Mammalia: Carnivora): a phylogenetic and evolutionary perspective. *Zoological Journal of the Linnean Society* 161: 414-462.
- Slater, G.J.; Van Valkenburgh, B. 2009. Allometry and performance: the evolution of skull form and function in felids. *Journal of Evolutionary Biology* 22: 2278-2287.

- Slice, D.E. 1993. Extensions, Comparisons, and Applications of Superimposition Methods for Morphometric Analysis. PhD Thesis: Department of Ecology and Evolution, State University of New York, Stony Brook.
- Smith, J.E.; Swanson, E.M.; Reed, D.; Holekamp, K.E. 2012. Evolution of Cooperation among Mammalian Carnivores and its Relevance to Hominin Evolution. *Current Anthropology* 53(S6): S436-S452.
- Smith, K.K. 2001. The evolution of mammalian development. *Bulletin of the Museum of Comparative Zoology* 156: 119-135.
- Somers, K.M. 1986. Multivariate allometry and removal of size with principal components analysis. *Systematic Zoology* 35: 359-368.
- Somers, K.M. 1989. Allometry, Isometry and Shape in Principal Components Analysis. *Systematic Zoology* 38 (2): 169-173.
- van Staaden, M.J. 1994. *Suricata suricatta*. *Mammalian Species* 483: 1-8.
- Steppan, S.J. 1997a. Phylogenetic analysis of phenotypic covariance structure. II. Reconstructing matrix evolution. *Evolution* 51(2): 587-594.
- Steppan, S.J. 1997b. Phylogenetic analysis of phenotypic covariance structure. I. Contrasting results from Matrix Correlation and Common Principal Component Analyses. *Evolution* 51(2): 571-586.
- Steppan, S.J.; Phillips, P.C.; Houle, D. 2002. Comparative quantitative genetics: Evolution of the G matrix. *Trends in Ecology & Evolution* 17(7): 320-327.
- Taylor, P.J.; Meester, J. 1993. *Cynictis penicillata*. *Mammalian Species* 432: 1-7.
- Trigo, T.C.; Schneider, A.; Oliveira, T.G.; Lehugeur, L.M.; Silveira, L.; Freitas, T.R.O.; Eizrik, E. 2013. Molecular Data Reveal Complex Hybridization and a Cryptic Species of Neotropical Wild Cat. *Current Biology* 23: 1-6.
- Turelli, M. 1988. Phenotypic evolution, constant covariances, and the maintenance of additive variance. *Evolution* 42(6): 1342-1347.
- Turner, A.; Antón, M.; Werdelin, L. 2008. Taxonomy and evolutionary patterns in the fossil Hyainidae of Europe. *Geobios* 41: 677-687.
- Van Valen, L.M. 1974. Multivariate structural statistics in natural history. *Journal of Theoretical Biology* 45: 235-247.
- Van Valkenburgh, B. 2007. Déjà vu: the evolution of feeding morphologies in the Carnivora. *Integrative and Comparative Biology* 47(1): 147-163.
- Veron, G.; Colyn, M.; Dunham, A.E.; Taylor, P.; Gaubert, P. 2004. Molecular systematics and origin of sociality in mongooses (Herpestidae, Carnivora). *Molecular Phylogenetics and Evolution* 30: 582-598.
- Veron, G.; Patou, M.-L.; Debruyne, R.; Couloux, A.; Fernandez, D.A.P.; Wong, S.T.; Fuchs, J.; Jennings, A.P. 2015a. Systematics of the Southeast Asian mongooses (Herpestidae, Carnivora): solving the mystery of the elusive collared mongoose and Palawan mongoose. *Zoological Journal of the Linnean Society* 173: 236-248.
- Veron, G.; Patou, M.-L.; Jennings, A.P. 2015b. Molecular systematics of the small-toothed palm civet (*Arctogalidia trivirgata*) reveals a strong divergence of Borneo populations. *Mammalian Biology* 80(40): 347-354.
- Veron, G.; Patou, M.-L.; Tóth, M.; Goonatilake, M.; Jennings, A.P. 2014. How many species of *Paradoxurus* civets are there? New insights from India and Sri Lanka. *Journal Zool Syst and Evol Research* 53(2): 161-174.
- Waitt, D.E.; Levin, D.A. 1998. Genetic and phenotypic correlations in plants: a botanical test of Cheverud's conjecture. *Heredity* 80: 310-319.
- Walker, J.A. 2000. Ability of Geometric Morphometric Methods to Estimate a Known Covariance Matrix. *Systematic Biology* 49(4): 686-696.
- Wang, E. 2002. Diets of ocelots (*Leopardus pardalis*), margays (*L. wiedii*) and oncillas (*L. tigrina*) in Southeast Brazil. *Studies on Neotropical Fauna and Environment* 37: 207-213.
- Werdelin, L. 1983. Morphological patterns in the skulls of cats. *Biological Journal of the Linnean Society* 19: 375-391.
- Whitlock, M.C.; Phillips, P.C.; Fowler, K. 2002. Persistence of changes in the genetic covariance matrix after a bottleneck. *Evolution* 56(10): 1968-1975.
- Wilting, A.; Buckley-Beason, V.A.; Feldhaar, H.; Gadau, J.; O'Brien, S.J. Linsenmair, K.E. 2007. Clouded leopard phylogeny revisited: support for species recognition and population division between Borneo and Sumatra. *Frontiers in Zoology* 4:15.
- Wood, B.; Collard, M. 1999. The human genus. *Science* 284: 65-71.
- Wozencraft, W.C. 1984. A phylogenetic reappraisal of the Viverridae and its relationship to other Carnivora. PhD Thesis, University of Kansas, Lawrence, KS.
- Wozencraft, W.C. 2005. Order Carnivora. In: *Mammal Species of the World, Third Edition*.

Wilson, D.E.; Reeder, D.M. (eds). The Johns Hopkins University Press, Baltimore: 532-628.

Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16: 97-159

Wroe, S.; Milne, N. 2007. Convergence and remarkably consistent constraint in the evolution of Carnivore skull shape. *Evolution* 61(5): 1251-1260.

Zeng, Z.B. 1988. Long-term correlated response, interpopulation covariation and interspecific allometry. *Evolution* 42: 363-374.

Zhang, J. 2003. Evolution of the Human ASPM Gene, a Major Determinant of Brain Size. *Genetics* 165: 2063-2070.

Capítulo 3: Conclusões Gerais

Este capítulo realiza um fechamento dos temas tratados na dissertação, considerando aquilo que fornece em relação às hipóteses específicas utilizadas como base para sua realização, discutindo como o trabalho como um todo contribui para o conhecimento sobre a área e indicando planos para publicação dos temas discutidos aqui, bem como possíveis direções futuras de investigação.

Hipóteses à luz dos resultados obtidos

Objetivos 1 e 3 - Aspecto 1 - Padrões de Integração.

Hipótese: Padrões de integração similares entre clados

A similaridade par-a-par entre matrizes **P** de Feliformia mostra valores médios consideravelmente altos para as 63 matrizes em nível de espécie (0.734) e para as 53 matrizes melhor estimadas (0.777), enquanto as menores similaridades encontradas no conjunto de 53 matrizes têm valores medianos (por volta de 0.5), comparáveis às menores similaridades encontradas em trabalhos prévios sobre padrões de integração em mamíferos (Porto *et al*, 2009, ordens de mamíferos; Oliveira *et al*, 2009, Catarrhini; Rossoni, 2013, Phyllostomidae). Ainda, as menores similaridades encontradas no conjunto de 53 matrizes geralmente envolvem também matrizes com amostra relativamente reduzida, sugerindo que os padrões de integração em Feliformia sejam ainda mais conservados que o indicado segundo os menores valores de similaridade obtidos. Dessa forma, a ideia de que seleção estabilizadora interna, com preservação do desenvolvimento e das funções gerais do crânio, mantenha os padrões de covariância preservados (Cheverud, 1996; Marroig & Cheverud, 2001; Porto *et al*, 2009), parece valer também para Feliformia. É interessante notar, porém, que mesmo com grande similaridade entre as matrizes de covariância, os padrões de integração mostram uma estruturação entre grupos, havendo diferenças entre Felidae, Prionodontidae, Hyaenidae e as famílias Viverridae e Herpestidae, cada uma desses grupos apresentando padrões mais similares internamente, mas relativamente menores entre grupos. A família Eupleridae, por outro lado, parece apresentar variação relativamente maior. Dessa forma, apesar de o processo de desenvolvimento comum de mamíferos levar à manutenção dos padrões de integração também em Feliformia, algumas diferenças são encontradas. Estas diferenças relacionam-se, em parte, às magnitudes de integração (associadas à variação de tamanho, provavelmente representando mudanças na última

parte do processo de desenvolvimento) e à própria morfologia média, como se descreve mais abaixo.

Assim, os padrões de integração em Feliformia mostram-se de fato bastante similares entre clados, de forma que a hipótese prévia para os padrões de integração é corroborada. Isso ocorre ainda que exista, simultaneamente uma estruturação dos padrões de integração entre grupos.

Objetivos 1 e 3 - Aspecto 2 - Magnitudes de integração.

Hipótese: Magnitude de integração mais variável entre clados

A magnitude de integração foi analisada utilizando o índice r^2 (van Valen, 1974), que mostrou alta correlação com o índice ICV (Shirai & Marroig, 2010), sugerindo resultados equivalentes entre os índices. A comparação da magnitude de integração em Feliformia utilizou as 53 matrizes representando táxons mais bem-estimados para reduzir possíveis efeitos decorrentes de números amostrais muito baixos. Um teste realizado com estas matrizes mostrou pequena influência do número amostral sobre a precisão, mas nenhum viés sistemático sobre as estimativas de r^2 (**Anexo 11**, em inglês). Os valores de r^2 encontrados indicam que há, de fato, variação considerável na magnitude de integração entre os representantes de Feliformia analisados. A etapa mais tardia do desenvolvimento, correspondente ao crescimento somático, produz covariação geral entre todas as partes do crânio (Hallgrímsson *et al*, 2007), ainda que essa covariação tenha maior intensidade em certas regiões, principalmente na face, cujo crescimento durante esta etapa é maior (Cheverud, 1995). A variação existente nas magnitudes de integração, portanto, provavelmente reflete, em grande parte, uma variabilidade no início e no tempo de duração do processo de crescimento somático entre os diferentes representantes de Feliformia. É interessante notar, entretanto, que parece haver uma estruturação da magnitude de integração entre diferentes grupos de Feliformia. . Particularmente, a família Felidae apresenta valores de integração geralmente mais altos, enquanto *Prionodon* e as famílias Viverridae, Herpestidae e Hyaenidae têm valores mais baixos. Apesar desses padrões gerais, ocorrem variações notáveis também internamente a esses grupos, como se nota na alta integração do viverrídeo *Paradoxurus musanga* e a integração relativamente baixa em três felídeos. Por fim, a magnitude de integração média entre as 53 matrizes melhor estimadas foi de 0.187, aproximando-se dos valores encontrados por Porto *et al* (2009) e Porto (2009) para *Leopardus* e para os representantes de Caniformia *Cerdocyon* e *Nasua* ($r^2 \sim 0.21$).

Assim, pode-se considerar que a hipótese de maior variação da magnitude de integração entre clados é corroborada em Feliformia, de forma concordante com o sugerido em Porto *et al* (2009), ainda que haja uma estruturação da magnitude de integração entre grupos.

Objetivo 1 - Aspecto 3 - Proporção de variação isométrica

Hipótese: Maior proporção de variação isométrica em Felidae em relação a outras famílias

A proporção de variação isométrica mostrou-se altamente correlacionada à magnitude de integração. Portanto, a estruturação descrita acima para as magnitudes de integração vale igualmente para a proporção de variação isométrica intra-específica dentro de cada grupo. Dessa forma, a hipótese de maior proporção de variação isométrica intra-específica em Felidae é corroborada. Isso sugere que a grande variação de tamanho, mas morfologia relativamente conservada descrita em comparações entre espécies em Felidae (e.g Werdelin, 1983; Christiansen, 2008; Sicuro, 2011; Sakamoto & Ruta, 2012) provavelmente reflete, pelo menos em parte, restrições decorrentes da organização da variação intra-específica. Ressalta-se entretanto que, como mencionado acima, este padrão geral de maior proporção de variação isométrica em Felidae não se verifica em todas as espécies da família. A verificação de um possível papel também de seleção alinhada a tamanho na diversificação de Felidae pode ser possível por meio de análises adicionais.

Objetivo 1 - Aspecto 4 - Padrões de resposta a seleção caráter-específicos

Sem hipótese a priori

Parte dos caracteres com padrões de resposta mais frequentemente distintos entre táxons para Feliformia como um todo (**Capítulo 2, Figura 2.8; Anexo 17**) coincide com caracteres para os quais foram também encontrados padrões distintos nos poucos outros trabalhos que utilizaram o método SRD (Hubbe, 2013; Costa, 2013; Rossoni, 2013). Os caracteres APET-TS e BA-OPI, ambos situados no basicrânio, foram reconhecidos como frequentemente distintos nos três trabalhos mencionados e também aqui; LD-AS (na abóboda craniana) foi reconhecido como tendo padrão de covariação distinto aqui, por Costa (2013; Sigmodontinae) e Rossoni (2013; Phyllostomidae), mas não em Xenarthra (Hubbe, 2013); BR-PT (abóboda craniana) aparece como distinto em Sigmodontinae (Costa, 2013) e em Feliformia; OPI-LD (abóboda) é distinto em Phyllostomidae (Rossoni, 2013) e Feliformia; e PT-TSP e BR-

LD (ambos na abóboda, com PT-TSP compartilhado com o zigomático) aparecem com padrões de resposta a seleção distintos em Xenarthra (Hubbe, 2013) e Feliformia. Por outro lado, o caráter ZS-ZI (na região zigomática), que mostra padrão de covariação distinto nos três grupos de mamíferos analisados previamente, mostra padrões distintos com frequência um pouco menor em Feliformia (pouco mais de 30% das comparações entre táxons), e OPI-LD (também na região da abóboda) é frequentemente distinto nas comparações entre táxons em Feliformia, mas não nos demais grupos. ;

Os resultados de SRD para Feliformia parecem mais uma vez mostrar que os caracteres cujo padrão de respostas a seleção mais difere entre espécies não apresentam uma correspondência clara entre diferentes grupos de mamíferos. Ainda assim, os resultados obtidos sugerem que caracteres nas regiões da base e abóboda craniana (neurocrânio) parecem ter maior tendência a mostrar padrões de covariação distintos entre táxons. Em particular, os caracteres BA-OPI e APET-TS, na base, consistentemente apresentaram padrões de resposta distintos entre espécies nos quatro grupos já analisados. Os resultados do presente trabalho mostram, ainda, que os caracteres mais frequentemente divergentes segundo o método SRD têm a similaridade em seus padrões de resposta entre espécies geralmente pouco correlacionada com a similaridade geral nos padrões de integração (*Random Skewers*). Desta forma, os caracteres identificados no SRD (em Feliformia concentrados na base e abóboda craniana) parecem mostrar variações em seus padrões de resposta de forma independente do restante do crânio. Portanto, estas regiões mais variáveis não parecem refletir estruturas mais gerais de similaridade e/ou divergência nos padrões de integração, como a estruturação separando felídeos, hienídeos, *Prionodon* e viverrídeos/herpestídeos.

Objetivo 2 - Aspectos 1 e 2 - Fatores relacionados a padrões e magnitudes de integração.

a) Padrão x magnitude

Sem hipótese a priori

Os resultados encontrados para Feliformia indicam uma associação entre padrões e magnitudes de integração (r^2) para a sub-ordem como um todo, bem como em diversos de seus subgrupos (superfamília Feloidea; família Felidae; subfamília Felinae; Herpestidae + Eupleridae segundo testes de Mantel), associação que, na maior parte dos casos, ocorre antes e após remover os efeitos da filogenia. Este resultado é similar ao

encontrado por Oliveira *et al* (2009) para os primatas do velho mundo, mas não ao de estudos em outros grupos de mamíferos, onde padrões e magnitudes não mostraram correlação significativa. Os resultados com métodos comparativos alternativos (PGLS e D-PGLS - **Anexo 16**) mostram que, para a subordem Feliformia como um todo, padrões de integração servem como preditores da magnitude de integração, e vice-versa. Mostram também que, para a família Herpestidae (em que uma relação entre padrões e magnitudes não foi reconhecida utilizando testes de Mantel), os padrões de integração servem como preditores da magnitude de integração, mas não o contrário. Ressalta-se que a associação encontrada entre padrões e magnitudes não é perfeita: o primeiro eixo de uma PCO sobre os padrões de integração é altamente correlacionado às magnitudes (r^2), mas felídeos têm valor consistentemente maior nesse eixo que espécies de outros grupos com valores similares de r^2 . Considerando que a magnitude de integração possivelmente reflete aspectos do processo de crescimento somático, é possível que a associação entre padrões e magnitudes de integração verificada aqui seja resultante de efeitos de uma alometria (i.e. crescimento somático diferencial entre os caracteres) similar em grande parte dos táxons, levando táxons com níveis similares de importância do crescimento somático (i.e. magnitudes de integração similares) a apresentar padrões de integração similares. Segundo esta interpretação, é possível que grupos díspares na relação encontrada entre padrões e magnitudes de integração (p.ex. Felidae e Hyaenidae) apresentem também padrões alométricos relativamente diferentes, produzindo seus padrões de integração mais distintos. Uma análise detalhada dos padrões alométricos de cada táxon, planejada para inclusão em uma das publicações resultantes da presente dissertação, pode ajudar a clarificar este aspecto..

b) Filogenia

Hipótese: Padrões de integração tendem a apresentar sinal filogenético em Feliformia.

Os resultados dos testes de Mantel verificando associação entre padrões de integração e filogenia comprovaram a existência de sinal filogenético na subordem Feliformia como um todo, bem como diversos subgrupos acima do nível de família (Feloidea, Viverroidea, Hyaenidae + Eupleridae + Herpestidae), mas não a partir do nível de família. Este resultado é condizente com a estruturação em grupos encontrada para os padrões de integração, com Felidae, Prionodontidae, Hyaenidae e Viverridae + Herpestidae (e a maioria dos representantes de Eupleridae) mostrando padrões relativamente distintos. Os resultados para o sinal filogenético utilizando métodos

alternativos (K/Kmult, **Anexo 16**) são condizentes com os encontrados usando testes de Mantel, com sinal filogenético identificado para padrões de integração em Feliformia, mas não para a família Herpestidae. Assim, a hipótese a priori de existência de sinal filogenético nos padrões de integração em Feliformia é corroborada.

A presença de sinal filogenético nos padrões de integração foi encontrada anteriormente em primatas do velho mundo (Oliveira *et al*, 2009), Xenarthra (Hubbe, 2013) e mais recentemente em Ruminantes por Haber (2015), que realiza uma análise mais detalhada indicando diferenças entre matrizes concentradas na divisão entre as famílias Bovidae e Cervidae. A existência de sinal filogenético em Feliformia como um todo, encontrada no presente trabalho, reflete o resultado encontrado previamente por Goswami (2006). Essa autora, entretanto, encontra uma relação entre padrões de integração e filogenia também dentro da família Felidae (somente quando utilizando distâncias filogenéticas calculadas com tamanhos de ramo iguais a 1, i.e. distâncias entre nós ou patrísticas), o que não se verifica aqui. Esta diferença pode se dever à utilização de distâncias patrísticas no trabalho de Goswami (2006), mas não aqui, ou talvez à maior representatividade filogenética incluída no presente trabalho.

A existência de sinal filogenético nos padrões de integração morfológica até o nível de família, mas não abaixo deste reforça a existência de uma estruturação da covariação na subordem Feliformia. As diferenças existentes entre famílias nos padrões de integração refletem sua história evolutiva compartilhada, e indicam que, além da restrição nos padrões de variação que parece existir para mamíferos como um todo, a integração mostra-se também relativamente restrita internamente às famílias - possivelmente refletindo particularidades funcionais ou no desenvolvimento de cada um desses grupos dentro do padrão geral compartilhado entre elas.

Sem hipótese a priori - Magnitudes de integração

Análises realizadas aqui utilizando testes de Mantel indicaram existência de sinal filogenético significativo em Feliformia como um todo e no subgrupo Feloidae (Felidae + Prionodontidae), mas não nos demais subgrupos. Este resultado reflete parcialmente a aparente estruturação das magnitudes de integração entre famílias, mencionado acima (ver também **Capítulo 2, Figura 2.6**), em que se nota, a despeito de variação considerável, magnitudes de integração geralmente maiores em Felidae e intermediários ou menores nas demais famílias. Os resultados encontrados com métodos

alternativos (K/Kmult, **Anexo 16**) coincidem com os testes de Mantel, mostrando sinal filogenético significativo em r^2 para Feliformia, mas não para a família Herpestidae.

A presença de associações significativas entre magnitudes de integração e filogenia foi encontrada anteriormente também em Xenarthra (Hubbe, 2013) e entre diferentes ordens de mamíferos (Porto *et al*, 2009), mas não em outros grupos de mamíferos já analisados (Oliveira *et al*, 2009; Costa, 2013, Rossoni, 2013), e possivelmente reflete uma estruturação entre grupos também do processo de crescimento somático, responsável por grande parte da covariação geral dentro do crânio (Hallgrímsson *et al*, 2007).

c) Morfologia

Sem hipótese a priori

Segundo os resultados de teste de Mantel, os padrões de integração mostraram-se correlacionados com a morfologia média em Feliformia como um todo e em grande parte dos subgrupos analisados (exceções sendo Pantherinae, Viverridae e Eupleridae; neste último caso, o valor da correlação encontrado foi bastante alto, mas não significativo). Os resultados obtidos com métodos alternativos (PGLS/D-PGLS; **Anexo 16**) mostram correlação significativa entre estes fatores para Feliformia como um todo, mas não para Herpestidae (em que a correlação encontrada por Mantel, apesar de considerada significativa, é baixa). É interessante notar a relativa similaridade encontrada entre padrões de integração de táxons filogeneticamente distantes, mas convergentes em sua morfologia, como é o caso de *Paradoxurus musanga* e *Nandinia binotata*, bem como de *Cryptoprocta ferox* e representantes de Felidae. Estas convergências nos padrões de integração, entretanto, não necessariamente representam uma regra geral, como sugere a maior proximidade da matriz tentativamente estimada para *Poiana richardsonii* a outros viverrídeos e não a representantes de *Prionodon*, nas comparações entre as 63 matrizes espécie-específicas. Associações entre padrões de integração e morfologia média foram encontrados antes para primatas do velho mundo (Oliveira *et al*, 2009), roedores sigmodontíneos (Costa, 2013) e morcegos filostomídeos (Rossoni, 2013), mas não para Xenarthra (Hubbe, 2013), e indicam uma evolução dos padrões de covariância associada à evolução das médias dos caracteres (por deriva ou seleção). Essa associação difere do que foi encontrado para os primatas neotropicais por Marroig & Cheverud (2001), em que as médias dos caracteres evoluíram independentemente dos padrões de integração, de forma condizente com uma

constância dos padrões de seleção estabilizadora e efeitos mutacionais, segundo o modelo de Lande (1980) - o que possivelmente não se verifica aqui para os diversos grupos em que existe correlação entre a evolução das médias morfológicas e dos padrões de covariância.

Os testes de Mantel identificaram também uma associação entre r^2 e a morfologia média para a subordem Feliformia como um todo, assim como para alguns de seus subgrupos (Feloidea, Felidae, Herpestidae + Eupleridae, Eupleridae). Em todos os casos exceto Eupleridae, essa relação se mantém após a correção para efeitos da filogenia. Os resultados utilizando métodos comparativos alternativos (**Anexo 16**) coincidem com os resultados utilizando Mantel, mas indicam que, utilizando uma regressão filogenética (D-PGLS), a morfologia é um bom preditor das magnitudes de integração, mas não o contrário. A presença de relação entre a morfologia média e as magnitudes de integração e também com padrões de integração em Feliformia possivelmente está ligada à existência de associação entre padrões e magnitudes no grupo, e mostra que a morfologia média e a integração tendem a evoluir, em diversas situações, de forma associada nesta subordem. Isto difere do que se observou para os demais grupos de mamíferos cuja integração morfológica já foi estudada, e indica que alterações ocorridas durante a história evolutiva do grupo influenciaram em algum nível alguns aspectos do desenvolvimento craniano juntamente com as médias dos caracteres.

d) Tamanho

Sem hipótese *a priori*

Os resultados encontrados para o tamanho absoluto do crânio (representado pelo logaritmo da média geométrica dos 35 caracteres utilizados) refletiram, em grande parte dos casos, o que se observou para a morfologia média. Este fato é esperado, uma vez que o método utilizado aqui para representar a morfologia média (distância de Mahalanobis entre táxons) trata simultaneamente tamanho e forma, o primeiro eixo de uma PCO realizada sobre as distâncias de Mahalanobis mostrando-se altamente correlacionado ao tamanho do crânio.. Por esta razão, associações entre a morfologia média e padrões e/ou magnitudes de integração podem resultar de relações da integração tanto com o formato dos crânios (i.e. "shape") quanto com seu tamanho. Nos casos em que os resultados obtidos para tamanho e morfologia média foram distintos, é possível realizar algumas inferências a respeito de qual aspecto da morfologia média (tamanho ou forma) está envolvido nas relações encontradas: em Hyaenidae +

Herpestidae + Eupleridae, Herpestidae + Eupleridae e na família Herpestidae, os padrões de integração mostram relação com a morfologia média, mas não com o tamanho médio. Assim, os padrões de integração nestes grupos provavelmente são influenciados pela forma média dos crânios, mas não por seu tamanho absoluto. Associações dos padrões e/ou magnitudes de integração com o tamanho do crânio, mas não com a morfologia média não foram encontradas em nenhum caso. Nos casos em que se encontra relação de padrões e/ou magnitudes de integração tanto com o tamanho do crânio quanto com a morfologia média, as alterações na integração associadas ao tamanho possivelmente decorrem de necessidades de integração distintas em determinadas partes do crânio para manutenção da funcionalidade com tamanhos cranianos diferentes.

Uma forma de avaliar de forma mais detalhada a influência da forma média e do tamanho sobre a integração morfológica seria utilizar métodos que permitem representar estes fenômenos independentemente. A utilização de métodos de morfometria geométrica seria uma possibilidade de fazê-lo, mas como mencionado na introdução seu uso em estudos lidando com integração é problemático. Outra abordagem possível seria a utilização de métodos de separação entre tamanho e forma ("shape and size"; ver p.ex. Bookstein, 1989) como o proposto por Mosimann (1970), que serviu como base para o método utilizado aqui para o cálculo da variação isométrica intra-específica.

e) Dieta

Hipótese: Variações de dieta tendem a estar relacionadas a diferenças nos padrões de integração, principalmente em regiões mais diretamente relacionadas à obtenção de alimento e mastigação (regiões oral e zigomática).

Os testes de Mantel identificaram uma relação entre a dieta e os padrões de integração em dois casos: para Feliformia como um todo antes de remover os efeitos de proximidade filogenética; e na família Herpestidae após corrigir os efeitos da filogenia. Desta forma, a relação entre dieta e padrões de integração encontrada para a subordem como um todo aparentemente reflete divergências conjuntas em dieta e integração ao longo da história evolutiva de Feliformia, mas não uma influência direta da dieta nos padrões de integração em grupos menos inclusivos. De forma condizente com este resultado, na maior parte dos subgrupos de Feliformia a dieta não parece exercer influência sobre os padrões de integração. Para os mangustos (Herpestidae), entretanto, a dieta parece ser um fator que influencia os padrões de integração de forma

significativa, atuando de forma indireta, por meio de pressões funcionais sobre as médias dos caracteres que terminam por afetar também as covariâncias, ou talvez diretamente por meio de seleção atuando sobre os próprios padrões de integração para atingir padrões de integração funcional ou de desenvolvimento distintos. O presente trabalho, portanto, identifica relações entre dieta e padrões de integração em Feliformia não verificados no estudo anterior de Goswami (2006), que utilizou em seu trabalho um conjunto de dados com representatividade reduzida de famílias de Feliformia além de Felidae.

As análises dos caracteres cranianos cujos padrões de covariação mostram maior relação com a dieta (após remoção dos efeitos da filogenia) mostra que efeitos mais fortes da dieta são encontrados em caracteres da região oral, como esperado, mas também em caracteres da abóboda craniana, tanto para Feliformia como um todo quanto para a família Herpestidae (Capítulo 2, Figuras 2.9 e 2.10). A relação da dieta com a covariação de caracteres da região da abóboda poderia estar ligada a aspectos funcionais, já que partes dessa região craniana constituem o local de origem de musculatura envolvida no processo de mastigação (*temporalis* - Done *et al*, 2009). Por outro lado, a sub-região do zigomático, também de grande importância para a mastigação, tem seus padrões de resposta a seleção sofrendo menor influência da dieta.

Sem hipótese *a priori* - Magnitudes de integração

Associações entre a dieta e as magnitudes de integração foram testadas previamente somente em dois estudos (Hubbe, 2013; Rossoni, 2013), que não encontraram relação entre estes fatores. O presente estudo tampouco encontra uma relação entre dieta e magnitudes de integração para a subordem Feliformia como um todo, bem como para a grande maioria de seus grupos. Tal relação foi encontrada, entretanto, para um subgrupo particular: a subordem Felinae (gatos de pequeno porte). A presença de influência da dieta sobre a magnitude de integração poderia ter relação com necessidades diferenciais de integração em determinadas partes do crânio para utilizar determinados tipos de alimento, ou ainda por razões associadas à atividade de captura de presas. Como a família Felidae praticamente toda é composta por espécies hipercarnívoras, a relação encontrada em Felinae necessariamente se baseia em diferenças relativamente pontuais na dieta, como a proporção de diferentes tipos de vertebrados na dieta, ou o consumo de frutos por *Leopardus wiedii* (Konecny, 1989; Wang, 2002). Considerando a existência de uma pressão geral em Felidae relacionada à

hipercarnivoria para manutenção de uma morfologia conservada (e possivelmente também de um padrão de integração conservado), é possível que a ausência de relação entre dieta e magnitude de integração em Pantherinae se deva à menor variação dietária encontrada entre os grandes felinos. As alterações na magnitude de integração poderiam também estar relacionadas a uma associação indireta entre a dieta e a magnitude de integração por meio de outros caracteres relacionados à história natural dos pequenos felinos, relacionados mais diretamente à variação de tamanho. Estudos futuros relacionando a dieta (ou aspectos específicos da dieta) à integração em diferentes partes do crânio (i.e. modularidade) poderão ajudar a compreender melhor a relação entre magnitude de integração e dieta encontrada aqui em Felinae.

f) Socialidade

Hipótese: Variações nos comportamentos sociais tendem a se relacionar a diferenças nos padrões de integração principalmente na região do neurocrânio (subregiões da abóboda craniana e do basicrânio).

Os resultados dos testes de Mantel mostraram que os padrões de comportamentos sociais não têm associação significativa com padrões de integração para a subordem Feliformia como um todo, nem na maior parte de seus subgrupos, ainda que o tamanho e a morfologia média mostrem relações com a socialidade, possivelmente refletindo, em parte, pressões para aumento no tamanho cerebral em espécies mais sociais, como esperado pela hipótese do cérebro social (Dunbar, 1998).. A análise dos padrões de resposta a seleção caráter-específicos mostra, entretanto, que a covariação em alguns caracteres particulares parece estar relacionada à socialidade em Feliformia como um todo. Estes incluem dois caracteres na abóboda craniana (PT-BA e PT-AS), possivelmente ligados ao tamanho do caixa craniana, e portanto potencialmente afetados pelo processo de crescimento do cérebro, mas também caracteres das regiões oral (e.g. MT-PNS) e zigomática (ZS-ZI e ZI-ZYGI).

Diferentemente do que ocorre em Feliformia e na maior parte de seus subgrupos, uma relação significativa entre socialidade e padrões de integração é encontrada nos mangustos (Herpestidae). Este fator, na verdade, é aquele que mostra maior correlação com os padrões de integração nesta família, que inclui diversos representantes sociais. A relação entre socialidade e padrões de integração em Herpestidae mantém-se mesmo após correção para os efeitos da filogenia, o que é particularmente relevante já que a maior parte das espécies sociais dessa família constitui um grupo monofilético (Veron

et al, 2004). Considerando que a morfologia média também mostra correlação com a socialidade em Herpestidae, a influência desse fator ecológico sobre a integração morfológica possivelmente se dá por meio de pressão seletiva (possivelmente relacionada em parte a um aumento da capacidade cerebral) atuando sobre as médias morfológicas e indiretamente afetando também as covariâncias. A análise com o método SRD em Herpestidae mostra correlações com a socialidade significativas e de valores medianos em diversos caracteres da abóboda craniana, que se esperaria serem mais diretamente afetados pela socialidade segundo a hipótese do cérebro social. Entretanto, correlações significativas e altas são encontradas também entre SRD e socialidade para caracteres na região da face (zigomático e região oral) - possivelmente em parte como resultado da correlação existente em Herpestidae entre dieta e socialidade.

É particularmente interessante a alta correlação existente entre SRD e socialidade em Herpestidae para um caráter no basicrânio (BA-APET) que possivelmente se relaciona com o nível de flexão do basicrânio, uma característica ligada ao tamanho do cérebro em primatas (Gould, 1977; Ross & Ravosa, 1993; Ross & Henneberg, 1995; Lieberman *et al*, 2000). Estes resultados para Herpestidae parecem mostrar que a socialidade pode - ao menos em grupos altamente sociais como é o caso dos mangustos - de fato exercer influência sobre os padrões de covariância do crânio, possivelmente por meio de uma relação entre a socialidade e o alterações no processo de crescimento do cérebro, como proposto pela *social brain hypothesis* (Dunbar, 1998).

Sem hipótese *a priori* - Magnitudes de integração

Testes de Mantel buscando associações entre magnitudes de integração e socialidade, realizados aqui de forma tentativa, encontraram relações entre esses fatores em dois subgrupos de Feliformia: Feloidea (Felidae + Prionodontidae) e a família Felidae (mas não internamente a cada às subfamílias Felinae e Pantherinae). Os representantes sociais desses grupos restringem-se à família Felidae, incluindo os panteríneos *Panthera leo* (grande e altamente social) e *Panthera uncia* (grande, somente caça em grupo) e os felíneos *Acinonyx jubatus* (grande, caça e defende território em grupo), *Felis catus* (pequeno, defende território e apresenta cuidado parental compartilhado), *Lynx canadensis*, *Lynx lynx* e *Lynx rufus* (tamanhos médios, somente caçam em grupo). Uma verificação das características dessas espécies mostra que a relação entre r^2 e socialidade em Feloidea e Felidae possivelmente ocorre devido à associação de ambos esses fatores com o tamanho do crânio. É possível, portanto, que a

associação entre r^2 e socialidade nesses grupos reflita somente o fato de que a maior parte das espécies sociais nesses grupos têm tamanhos corpóreos maiores (ainda que nem todos os felídeos grandes apresentem socialidade). Alterações na magnitude de integração resultando de um processo mais intenso de crescimento somático por influência direta da socialidade parece bastante improvável, já que a região do neurocrânio (e em especial a abóboda craniana) cresce relativamente menos que outras regiões durante esta etapa do desenvolvimento (Cheverud, 1995). Este resultado aponta a possível relevância de aprofundar análises dos fatores que podem influenciar a integração por meio de testes que considerem efeitos compartilhados entre fatores (e.g. testes de Mantel parciais removendo efeitos de fatores adicionais, como o tamanho no presente caso; ou PGLS/D-PGLS com modelos incluindo mais de um fator como variável preditora), permitindo identificar com maior precisão os fatores que afetam diretamente a evolução da morfologia craniana e da integração morfológica.

Conclusões finais e direções futuras

A presente dissertação se constrói sobre os resultados de trabalhos prévios sobre a evolução da integração fenotípica intra-populacional em mamíferos (Marroig & Cheverud, 2001; Goswami, 2006; Porto *et al*, 2009; Oliveira *et al*, 2009; Shirai & Marroig, 2010; Hubbe, 2013; Costa, 2013; Rossoni, 2013; Haber, 2015), representando a investigação deste tema com maior representatividade taxonômica e realizada até o presente momento na subordem Feliformia e em Carnivora como um todo. A amostra utilizada aqui praticamente duplica o número de táxons representado no maior trabalho anterior tratando sobre a integração morfológica em Carnivora (Goswami, 2006). e utiliza um número amostral total cinco vezes maior, permitindo assim estimativas mais robustas para matrizes **P** de diversos táxons e comparações mais detalhadas abarcando a diversidade existente em Feliformia.

Os resultados obtidos reforçam conclusões anteriores de Porto *et al* (2009), com similaridade geralmente alta nos padrões de integração e variação maior nas magnitudes de integração. Ao mesmo tempo, a observação do "espaço de integração" e os resultados de testes de associação entre padrões de integração e filogenia indica uma estruturação dos padrões de covariação de acordo com agrupamentos taxonômicos/filogenéticos, com quatro grupos mostrando padrões de integração relativamente mais similares entre si que com outros grupos (famílias Felidae, Hyaenidae e Prionodontidae, e um agrupamento de Viverrídeos com Herpestídeos e

grande parte dos Euplerídeos), estruturação que parece comparável a uma parte dos resultados encontrados por Haber (2015). Essa autora, utilizando métodos comparativos diferentes daqueles usados aqui, argumenta que a existência de diferenças entre matrizes maiores que as esperadas por movimento browniano (inclusive internamente a cada família) possivelmente tornaria inviável o uso de análises baseadas em métodos que dependem de estabilidade nas matrizes de covariância. Argumenta-se aqui, entretanto, que apesar da estruturação em grupos encontrada (aqui e em Haber, 2015), a grande similaridade existente nos padrões de covariância mesmo entre táxons de grupos distintos é condizente com a interpretação dos padrões de covariância como bastante conservados, possivelmente mantidos por seleção estabilizadora interna (Cheverud, 1996; Marroig & Cheverud, 2001; Porto *et al*, 2009), o que provavelmente permite a realização de estudos baseados em Lande (1979) utilizando matrizes **P** de Feliformia. Ressalta-se, apesar disso, que a obtenção futura de uma matriz **G** para Carnívora e sua comparação com matrizes **P** do grupo seria uma empreitada interessante e poderia reforçar esta conclusão, uma vez que as únicas comparações já realizada entre matrizes genéticas e carnívoros foram realizadas com uma matriz **G** de roedores (Porto, 2009; Porto *et al*, 2009).

Diferentemente do que se observou para outros grupos de mamíferos, parece ocorrer ao menos em partes de Feliformia uma coordenação entre as mudanças na morfologia média, nos padrões e magnitudes de integração. Esta coordenação leva a padrões e magnitudes de integração similares entre táxons filogeneticamente distantes, mas morfologicamente convergentes, como é o caso de felídeos e fossas (*Cryptoprocta*, família Eupleridae), bem como de um viverrídeo (*Paradoxurus musanga*) e o único representante da família basal Nandiniidae (*Nandinia binotata*). A associação entre integração e morfologia média não é direta, havendo diferenças relevantes nos padrões de integração entre táxons com mesma magnitude de integração, em particular entre representantes da família Felidae, da subfamília Hyaeninae e membros de outras famílias. Nota-se também que vários táxons com morfologia convergente tendem a mostrar padrões e/ou magnitudes de integração similares. O cálculo explícito da proporção de variação isométrica intra-específica mostrou grande correlação desta com a magnitude de integração, como mostrado em Porto *et al* (2013) para o tamanho medido pelo PC1. Magnitude de integração e variação isométrica mostram ainda valores médios mais altos em Felidae que nas demais famílias, indicando que a grande variação de tamanho e morfologia conservada observada entre espécies para Felidae (e.g

Werdelin, 1983; Christiansen, 2008; Sicuro, 2011; Sakamoto & Ruta, 2012) possivelmente reflete, ao menos em parte, restrições devidas à estrutura de variação intra-específica.

Os testes de associação com a filogenia identificaram sinal filogenético significativo em padrões e magnitudes de integração, bem como na morfologia média para o grupo como um todo. Para o padrão de integração, particularmente, reconheceu-se sinal filogenético significativo na maior parte dos agrupamentos acima do nível de família, mas em nenhum a partir deste nível, dando suporte à estruturação dos padrões de covariação em grupos e sugerindo uma restrição dos padrões de integração no nível de família. A utilização de métodos alternativos que permitam reconhecer os pontos específicos da filogenia em que se concentra a maior parte da variação nos padrões e magnitudes de integração (Pavoine *et al*, 2010; Jombart *et al*, 2010; possivelmente outros) pode representar uma direção interessante para trabalhos futuros, permitindo análises mais detalhadas da diversificação da integração ao longo da história evolutiva de Feliformia.

Esta dissertação identifica a relevância de dois fatores que parecem ter influenciado a evolução da integração fenotípica ao menos em partes de Feliformia. A dieta mostrou-se correlacionada com os padrões de integração morfológica para a subordem como um todo antes de remover os efeitos da filogenia. Isto, junto à existência de sinal filogenético tanto para dieta quanto para padrões de integração, parece indicar alterações associadas na dieta e na integração ao longo da filogenia do grupo, ainda que não haja influência direta da dieta sobre a integração dentro de cada um dos subgrupos de Feliformia. Este resultado é discordante daquele mostrado por Goswami (2006), e ilustra a relevância de representar da melhor forma possível a diversidade de um grupo na realização de análises comparativas. Entre os mangustos (Herpestidae), particularmente, tanto a dieta quanto a socialidade correlacionam-se significativamente com os padrões de covariação, demonstrando pela primeira vez a possibilidade de influência da socialidade sobre a integração morfológica e mostrando que diferentes fatores podem afetar de formas variadas o fenômeno complexo de organização da covariação no crânio.

A análise focada nos padrões caráter-específicos de resposta à seleção mostrou que, ainda que não se reconheça uma associação significativa entre socialidade e integração para Feliformia como um todo, os padrões de covariação de alguns caracteres particulares (parte dos quais possivelmente influenciados pelo processo de

crescimento do cérebro) parecem ser influenciados por este aspecto da ecologia. Mostrou, também, que dieta e socialidade aparentemente afetam a covariação tanto de caracteres cuja relação funcional com esses fatores ecológicos parece ser mais direta (região oral para dieta; abóboda e basicrânio para a socialidade), quanto também de outras regiões. O zigomático, em particular, parece ser afetado em algum nível tanto por dieta quanto por socialidade. Estes resultados mostram a importância de considerar diferentes fatores que podem afetar a evolução da integração morfológica, e ao mesmo tempo indicam a relevância de tentar considerar simultaneamente influências conjuntas de diferentes fatores sobre a integração, permitindo a identificação de quais fatores mais diretamente afetam a integração morfológica. Isto talvez possa ser feito, por exemplo, utilizando conjuntos de testes de Mantel parciais corrigindo para efeitos de diferentes fatores, ou simultaneamente incluindo fatores distintos em regressões filogenéticas multivariadas (e.g. D-PGLS, Adams, 2014a), o que necessariamente implicaria representar cada fator por um conjunto menor de variáveis/eixos.

Uma análise preliminar realizada no presente trabalho (**Anexo 16**) mostra uma concordância geral entre os resultados de diferentes métodos filogenéticos comparativos (testes de Mantel e D-PGLS) e de diferentes métodos para a análise de sinais filogenéticos (Mantel e K/Kmult - Adams, 2014b). Apesar da concordância em diversos aspectos, a presença de alguns resultados díspares entre os métodos sugere a relevância de um trabalho futuro estendendo a análise realizada aqui para investigar de forma mais extensa e sistemática o uso de diferentes métodos comparativos e testes de métodos para reconhecer sinal filogenético e/ou formas de diversificação da integração ao longo da filogenia.

Uma outra possível direção futura de trabalho que se apresenta a partir dos resultados aqui obtidos é uma análise específica comparando integração morfológica, morfologia média e dieta em diversas linhagens dos três tipos principais de hipercarnívoros reconhecidos por Van Valkenburgh (2007) - "cat-like", "hyaena-like" e "cat-like", de grupos aparentados e de possíveis hipercarnívoros não pertencentes a esses ecomorfos tradicionais (ex. *Prionodon*; Davis, 1958; Lim, 1973; Wozencraft, 1984; Pham-Chong-Ahn, 1980). As convergências em morfologia e integração encontradas entre felinos e *Cryptoprocta* ("cat-like") e dentro da subfamília Hyaeninae ("hyaena-like"), mas não entre esses grupos, sugere a existência de estruturas distintas da integração em diferentes ecomorfos hipercarnívoros. O número de representantes de cada um desses ecomorfos analisados aqui torna essa sugestão

relativamente frágil; se possível, estudos incluindo outros táxons pertencentes a estes ecomorfos (bem como táxons "*wolf-like*") e grupos aparentados podem permitir análises mais detalhadas de aspectos relacionados à evolução da hipercarnivoria.

Dado o grande volume de informações e variedade de questões tratadas aqui, planeja-se publicar os resultados no futuro realizando uma divisão em ao menos três artigos: um tratando especificamente sobre as comparações e a estruturação de padrões e magnitudes de integração e da morfologia média em Feliformia; um segundo abordando a relação entre integração e filogenia e os fatores ecológicos que influenciam a evolução da integração morfológica em Feliformia; e um terceiro lidando especificamente com a isometria e alometria intra-populacional e variação intra-populacional não relacionada a tamanho. Para a publicação destes trabalhos, é provável que os dados e resultados de Feliformia apresentados aqui sejam combinados com dados de seu grupo irmão Caniformia, atualmente analisados em um projeto de Doutorado do Laboratório de Evolução de Mamíferos (Fábio de Andrade Machado; Bolsa FAPESP 11/21674-4). Planeja-se também aprofundar as análises de modularidade iniciadas no contexto do projeto que deu origem à presente dissertação, as quais devem dar origem a uma publicação adicional.

Referências

- Adams, D.C. 2014a. A method for assessing phylogenetic least squares models for shape and other high-dimensional multivariate data. *Evolution* 68(9): 2675-2688.
- Adams, D.C. 2014b. A generalized K statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data. *Systematic Biology* 63(5): 685-697.
- Bookstein, F.L. 1989. "Size and Shape": A Comment on Semantics. *Systematic Zoology* 38(2): 173-180.
- Cheverud, J.M. 1996a. Quantitative genetic analysis of cranial morphology in the cotton-top (*Saguinus oedipus*) and saddle-back (*Saguinus fuscicollis*) tamarins.
- Cheverud, J.M. 1995. Morphological integration in the saddle-back tamarin (*Saguinus fuscicollis*) cranium. *American Naturalist* 143: 63-89.
- Christiansen, P. 2008. Evolution of skull and mandible shape in cats (Carnivora: Felidae). *PLoS ONE* 3 (7): e2807
- Costa, B.M.A. 2013. Evolução e integração morfológica do crânio dos roedores da subfamília Sigmodontinae Wagner, 1843 (Rodentia, Cricetidae). Tese de Doutorado, Universidade de São Paulo.
- Davis, D.D. 1958. Mammals of the Kelabit Plateau, northern Sarawak. *Fieldiana Zoology* 39: 119-147.
- Done, S.H.; Goody, P.C.; Evans, S.A.; Stickland, N.C. 2009. Color Atlas of Veterinary Anatomy, Volume 3: The Dog and Cat. Elsevier Health Sciences.
- Dunbar, R.M. 1998. The social brain hypothesis. *Evolutionary Anthropology* 7: 178-190.
- Goswami, A. 2006a. Morphological integration in the carnivoran skull. *Evolution* 60 (1): 169-183.
- Gould, S.J. 1977. Ontogeny and Phylogeny. Cambridge: Belknap Press.
- Haber, A. 2015. The Evolution of Morphological Integration in the Ruminant Skull. *Evolutionary Biology* 42: 99-114.

- Hallgrímsson, B.; Lieberman, D.E.; Young, N.M.; Parsons, T.; Wat, S. 2007. Evolution of covariance in the mammalian skull. Novartis Foundation Symposium 284: 164-190.
- Hubbe, A. 2013. Análise morfológica craniana de *Xenarthra* atuais e extintos: inferências evolutivas e funcionais. Tese de Doutorado, Universidade de São Paulo.
- Jombart, T.; Pavoine, S.; Devillard, S.; Pontier, D. 2010. Putting phylogeny into the analysis of biological traits: A methodological approach. *Journal of Theoretical Biology* 264(3): 693-701.
- Konecny, M.J. 1989. Movement patterns and food habits of four sympatric carnivores species in Belize, Central America. *In*: Redford, K.H.; Eisenberg, J.F. (eds). *Advances in Neotropical Mammalogy*, pp 243-264. Sandhill Crane Press, Gainesville, Florida.
- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution* 33(1): 402-416.
- Lande, R. 1980. The genetic covariance between characters maintained by pleiotropic mutations. *Genetics* 94: 203-215.
- Liebermann, D.E.; Ross, C.F.; Ravosa, M.J. 2000. The primate cranial base: Ontogeny, function and integration. *Yearbook of Physical Anthropology* 43: 117-169.
- Lim, B.L. 1973. The banded linsang and the banded musang of West Malaysia. *Malayan Natural History Journal* 26: 105-111.
- Marroig, G.; Cheverud J.M.. 2001. A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology, and ontogeny during cranial evolution of new world monkeys. *Evolution* 55(12): 2576-600.
- Mosimann, J.E. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. *Journal of the American Statistical Association* 65: 930-945.
- Oliveira, F.B.; Porto, A.; Marroig, G. 2009. Covariance structure in the skull of Catarrhini: a case of pattern stasis and magnitude evolution. *Journal of Human Evolution* 56(4): 417-430.
- Pavoine, S.; Baguette, M.; Bonsall, M.B. 2010. Decomposition of trait diversity among the nodes of a phylogenetic tree. *Ecological Monographs* 80(3): 485-507.
- Phang-Chong-Ahn. 1980. A contribution to the morphology and ecology of the Viverridae (Mammalia) in Vietnam. *Zoologicheskii zhurnal* 59: 905-914.
- Porto, A. 2009. Evolução da modularidade no crânio de mamíferos. Dissertação de mestrado. Universidade de São Paulo.
- Porto, A.; Oliveira, F.B.; Shirai, L.T.; de Conto, V.; Marroig, G. 2009. The Evolution of Modularity in the Mammalian Skull I: Morphological Integration Patterns and Magnitudes. *Evolutionary Biology* 36:118-135.
- Porto, A.; Shirai, L.T.; Oliveira, F.B.; Marroig, G. 2013. Size variation, growth strategies and the evolution of modularity in the mammalian skull. *Evolution* 67(11): 3305-3322.
- Ross, C.F.; Henneberg, M. 1995. Basicranial flexion, relative brain size and facial kyphosis in *Homo sapiens* and some fossil hominids. *American Journal of Physical Anthropology* 98: 575-593.
- Ross, C.F.; Henneberg, M.; Ravosa, M.J.; Richard, S. 2004. Curvilinear, geometric and phylogenetic modeling of basicranial flexion: is it adaptive, is it constrained? *Journal of Human Evolution* 46: 185-213.
- Rossoni, D.M. 2013. Integração morfológica craniana em morcegos da Família Phyllostomidae. Tese de Doutorado, Universidade de São Paulo.
- Sakamoto, M.; Ruta, M. 2012. Convergence and Divergence in the Evolution of Cat Skulls: Temporal and Spatial Patterns of Morphological Diverity. *PLoS ONE* 7(7): e39752.
- Shirai, L.T.; Marroig, G. 2010. Skull modularity in neotropical marsupials and monkeys: size variation and evolutionary constraint and flexibility. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 314B(8): 663-683.
- Sicuro, F.L. 2011. Evolutionary trends on extant cat skull morphology (Carnivora: Felidae): a three-dimensional geometrical approach. *Biological Journal of the Linnean Society* 103: 176-190.
- Van Valen, L.M. 1974. Multivariate structural statistics in natural history. *Journal of Theoretical Biology* 45: 235-247.
- Van Valkenburgh, B. 2007. Déjà vu: the evolution of feeding morphologies in the Carnivora. *Integrative and Comparative Biology* 47(1): 147-163.
- Veron, G.; Colyn, M.; Dunham, A.E.; Taylor, P.; Gaubert, P. 2004. Molecular systematics and origin

of sociality in mongooses (Herpestidae, Carnivora).
Molecular Phylogenetics and Evolution 30: 582-598.

Wang, E. 2002. Diets of ocelots (*Leopardus pardalis*), margays (*L. wiedii*) and oncillas (*L. tigrina*) in Southeast Brazil. Studies on Neotropical Fauna and Environment 37: 207-213.

Werdelin, L. 1983. Morphological patterns in the skulls of cats. Biological Journal of the Linnean Society 19: 375-391.

Wozencraft, W.C. 1984. A phylogenetic reappraisal of the Viverridae and its relationship to other Carnivora. PhD Thesis, University of Kansas, Lawrence, KS.

Resumo

A integração morfológica determina a quantidade de variação disponível em diferentes direções do espaço multivariado entre um conjunto de caracteres, e pode assim ter importantes consequências evolutivas, enviesando a direção e a taxa de evolução morfológica em determinadas direções. Assim, estudar a evolução da integração morfológica é importante para entender a evolução fenotípica de uma linhagem. Neste trabalho, utilizo abordagens de genética quantitativa comparativa para estudar a evolução da integração morfológica no crânio em carnívoros da subordem Feliformia, grupo com extensa diversidade filogenética, morfológica e ecológica para o qual análises anteriores de integração analisaram número reduzido de espécies. Para este fim, comparo matrizes de covariância fenotípicas intra-populacionais quantificando a associação entre 35 distâncias lineares no crânio de um conjunto de táxons incluindo todas as sete famílias e mais de um terço da diversidade filogenética atual da subordem. Investigo também a associação entre integração morfológica e a evolução da morfologia média, assim como a influência da história evolutiva (filogenia) e de dois aspectos da ecologia (dieta e socialidade) sobre a evolução da morfologia média e da integração. Os padrões de integração fenotípica no crânio (i.e. quais caracteres variam em conjunto com maior intensidade) são bastante estáveis na subordem, como observado para outros mamíferos, mas revelam alguma sub-estruturação, com padrões um pouco distintos em Felidae, Hyaenidae e Prionodontidae. As magnitudes de integração são também relativamente estruturadas, com valores geralmente mais altos em Felidae e consistentemente mais baixos em Hyaenidae. Apesar disso, a magnitude geral de integração é evolutivamente plástica, como em outros mamíferos, havendo importantes variações internas a cada família. Encontrei uma associação geral entre a evolução da morfologia média e modificações em padrões e magnitudes de integração para a subordem como um todo e em vários grupos menos inclusivos, o que em alguns casos se manifesta como uma semelhança da integração entre táxons morfológicamente convergentes, mas filogeneticamente distantes. A evolução de padrões de integração se correlaciona à história filogenética em Feliformia como um todo e na maior parte dos grupos acima, mas não abaixo do nível de família, corroborando padrões de covariação relativamente distintos apesar de sua alta similaridade, bem como integração mais restrita internamente a cada

família. A dieta está associada à filogenia, e correlaciona-se à evolução da morfologia média e dos padrões de integração na subordem como um todo antes, mas não após correção levando em conta a proximidade filogenética, indicando que alterações na dieta são parte da história evolutiva compartilhada que levou às diferenças em morfologia média e integração existentes no grupo. Os caracteres cujos padrões de covariação estão mais associados à dieta na subordem incluem partes das regiões oral e zigomática, além de algumas partes do neurocrânio. A socialidade está relacionada à evolução da morfologia craniana média, mas não aos padrões de integração gerais em Feliformia, apesar de existirem associações entre a socialidade e os padrões de resposta a seleção de alguns caracteres específicos, incluindo partes do neurocrânio e distâncias ligadas ao arco zigomático. Os mangustos (família Herpestidae) mostraram influência significativa tanto da dieta quanto da socialidade na evolução de sua morfologia craniana média e de seus padrões de integração, ressaltando a importância desses dois aspectos ecológicos na evolução fenotípica do grupo e mostrando, pela primeira vez, uma associação direta entre a integração no crânio e o comportamento social, possivelmente intermediada por aspectos relacionados ao desenvolvimento do cérebro. O presente trabalho sugere, assim, uma complexa interação de fatores afetando a evolução da morfologia craniana em Feliformia, e indica direções para trabalhos futuros, incluindo análises dos padrões de modularidade craniana no grupo e, possivelmente, análises comparativas em diferentes morfotipos hipercarnívoros abordando a morfologia média e a integração morfológica no crânio, bem como a dieta e possivelmente outros fatores.

Abstract

Morphological integration determines the standing variation available within a lineage in different directions of the multivariate space of a trait set, and can therefore have important evolutionary consequences, biasing the direction and rate of morphological evolution in certain directions. Consequently, studying the evolution of morphological integration is important to understand a lineage's phenotypic evolution. Here I employ a comparative quantitative genetic framework to study the evolution of morphological integration in the skull for the suborder Feliformia (Carnivora), a group with remarkable phylogenetic, morphological and ecological diversity for which previous analysis of integration included a limited number of species. To this purpose, I compare within-population phenotypic covariance matrices quantifying the associations between 35 skull linear measurements in a set of taxa including all seven feliform families and over one third of the suborder's extant phylogenetic diversity. I also assess the association between morphological integration and the evolution of average skull morphology, as well as the influence of evolutionary history (phylogeny) and two ecological aspects (diet and sociality) on the evolution of average morphology and integration. Skull integration patterns (i.e. which characters covary the most) are quite stable in the suborder, as seen among other mammals, but also have some structuring between groups, with relatively distinct patterns in Felidae, Hyaenidae and Prionodontidae. Integration magnitudes are also relatively structured, with generally higher values in Felidae and consistently lower values in Hyaenidae. Nevertheless, the overall magnitude of integration is evolutionarily labile, as in other mammals, with important variations occurring within each family. I found a general association between the evolution of average morphology and changes in integration patterns and magnitudes for the suborder as a whole and also for many less inclusive groups, which in some cases leads to similar integration between morphologically convergent, but phylogenetically distant taxa. The evolution of integration patterns is correlated to phylogenetic history in Feliformia as a whole and in most groups above, but none below the family level, corroborating relatively distinct covariation patterns in spite of their high similarity, and also a greater constraint of integration within each family. Diet is associated to phylogeny, and correlates to the evolution of average morphology and integration

patterns in the suborder before, but not after correction for phylogenetic relatedness, indicating that dietary changes are part of the shared evolutionary history which shaped the differences in average morphology and integration existing in the group. The characters with covariation patterns more closely associated to diet include parts of the oral and zygomatic skull regions, as well as parts of the neurocranium. Sociality is related to the evolution of average skull morphology, but not to general integration patterns in Feliformia as a whole, although there are correlations between sociality and the selection response patterns of some specific characters, including parts of the neurocranium and measurements related to the zygomatic arch. Mongooses (family Herpestidae) had the evolution of their average skull morphology and integration patterns significantly influenced by both diet and sociality, stressing the importance of these two ecological factors for phenotypic evolution of this group and showing for the first time a direct association between morphological integration in the skull and social behaviour, possibly mediated by aspects related to brain development. The present work thus suggests a complex interaction of factors affecting the evolution of skull morphology in Feliformia, and opens up directions for future work, including analyses of skull modularity patterns in this group and, possibly, comparative analyses of different hypercarnivore morphotypes addressing average skull morphology and morphological integration, as well as diet and possibly other factors.

Appendices

Appendix 1- List of digitised specimens kept after removing outliers by species and museum.

Museum codes: AMNH: American Museum of Natural History (New York); MNHN: Muséum National d'Histoire Naturelle (Paris); MNRJ: *Museu Nacional da Universidade Federal do Rio de Janeiro*; MZUSP: *Museu de Zoologia da Universidade de São Paulo*; **Naturalis**: Naturalis Biodiversity Centre (Leiden); NMP: Přírodovědecké muzeum - Národní muzeum (Prague) NMW: *Naturhistorisches Museum Wien* (Vienna); SMF: Senckenberg Naturmuseum Frankfurt (Frankfurt am Main); UMZC: University Museum of Zoology Cambridge; ZFMK: Zoologisches Forschungsmuseum Alexander Koenig (Bonn); ZMB_Mam: Museum für Naturkunde (Berlin). Specimen codes may not correspond to final registry numbers in some cases. Codes are as presented on skulls and/or on the boxes where they were stored, or include notes regarding the skull when a code was not present.

Acinonyx jubatus MNRJ 24866, MZUSP TX050359, TX050001, NMP 46206, 46721, 46722, 46760, 46202, 47537, 46720, 47538, 50445, 48524, 48523, 58347, 47670, ZMB_Mam 56128, 56123, 46446, 46173, 34306, 56301, 56300, 56290, 56299, 56305, 56304, 56303, 56302, 56294, 56293, 56292, 56297, 46556, 56289, 56287, 56126, 6616, 1219, 56277, 56276, 12725, 16812, 56285, 16813, 91304, 93332, 82977

Arctictis binturong AMNH 106767, 107134, 90279, 103744, 106770, 181, 106768, 106769, 299, 106613, 87388, 80162, 119503, 90383, 80163, 119600, 35469, 22906, 19164, MNHN 1936-1529, 2005-844, 1871-103, 1883-1286, 1959-203, 1992-1487, 1990-88, 1976-331, 1898-96, 1975-78, NMW 1502, 4067, B, 1973/IR 214 (?), 5465, 40370, 12381, 15177, 1168, 1336, ZMB_Mam 8950, 797, 11685, 43666, 83042, 83046, 83044, 83047, 83048, Dummy 2718? (No Number), Keine Nummer - ursprünglich "Proteles cristatus"

Arctogalidia stigmatica AMNH 103740, 103998, 103741, 103742, 103708, 106059, 107129, 107130, 107127, 107128, 107125, 107126, 107123, 107124, 107121, 107122, 107057, 107120, 107055, 107056, 107053, 107054, MNHN 2001-495, **Naturalis** ZMA 1318, ZMA 10313, ZMA 1148, NMW B2036, ZMB_Mam 92187, 1163, 92188, 92189

Arctogalidia trivirgata AMNH 102700, 87379, 87378, 87377, 113489, 54776, MNHN 1998-1970, **Naturalis** ZMA 1322, ZMA 1323, ZMA 9867, RMNH 14597, RMNH 14571, NMW 40352, 5012, SMF 444, ZMB_Mam 42208, 83124 (2), 42209

Atilax paludinosus ZMB_Mam 35210, 82888, 1133, 31231, 18112, 44251, 82914, 82910, 82920, 82908, 82919, 82958, 82918, 82955, 82916, 82962, 31441, 9077, 82956, 82928, 82927, 5067, 40172, 40171, 82886, 1117, 82929, 82871, 82874, 82875, 82873, 82876, 82877, 82880, 46440, 20261, 82882, 82883, 82892, 82885, 82884, 82935, 82898, 82893, 82887, 82889, 82902, 82903, 82907, 82937

Bdeogale crassicauda AMNH 161766, MNHN 1881-1521

Bdeogale jacksoni AMNH 33334, 83226

Bdeogale nigripes AMNH 51582, 51581

Caracal aurata AMNH 89441, 51994

Caracal caracal AMNH 238456, 24220, 116512, 89841, 113594, 187788, 90105, MZUSP 32622, NMP 94213, 46546, 46756, SMF 55033, 15709, 62834, 16201, 51592, 16216, 53505, 55034, 266, 16217, ZMB_Mam 6436, 7519, 14860, 46196, 10907, 57823, 32410, 58025, 18152, 58024, 57814, 104690, 10367, 79167, 6190, 104691, Keine Nummer - aus aufgelöstem Praktikumsschrank 3.2011, 57825, 37733, 58019, 16047, 58021, 58022, 22065, 60964, 16484, 16814, 14859, 41739

Catopuma badia **Naturalis** RMNH 25534

Catopuma marmorata AMNH 106615, MNHN 1886-25

Catopuma temmincki AMNH 171037, 84396, 84394, 84393, 84395, MNHN 1865-488, 1881-1591, 1962-2927, 1932-3228, 1941-293, **Naturalis** ZMA 12381, ZMA 9674, ZMA 9531, ZMA 11624, ZMA 15067, RMNH 1902, RMNH 5049, RMNH No Number S 259, RMNH 5280, NMW 1446, 1475, 1476, 1445, SMF 16249, 47967, UMZC 6481, ZFMK 87-86, 50-728 (9), 72-355, 2002-487, 2002-488, 2011-1034, 91-333, 82-42, ZMB_Mam 47689, 91060, 4929, 53053, 13052, 7711

Chrotogale owstoni ZMB_Mam 105412

Civettictis civetta ZMB_Mam 45278, 68786, 68877, 68875, 68942, 68945, 68879, 68947, 68878, 68793, 68948, 68952, 68954, 68957, 68959, 68958, 68960, 68800, 68896, 68803, 68917, 68810, 68925, 68868, 68890, 68867, 68792, 68926, 68873, 68927, 68809, 68836, 48453, 68788, 68824, 68804, 68807, 68898, 68899, 68900, 19886, 68901, 68902, 68808, 68791, 68790, 68892, 68872, 43646, 41547, 1959

Crocota crocuta ZMB_Mam 60994, 82419, 82398, 82412, 15859 (2), 82406, 73148, 82435, 7884 (1), 14820, 82472, 82436, 82399, 41225, 82497, 82498 (auf Schädel) -anderer?, 82489, 41224, 48206, 82400, 7593, 82410 (auf Schädel)/82498?, 82553, 82437, 29296, 82413, 18187, 82405, 82461, 82415, 46123, 82407, 13295, 82484, 82483, 82487, 82462, 82453, 82471, 44089, 82476, 82474, 82480, 82473, 82390, 82396, 82392, 82389, 82425, 82402

Crossarchus alexandri AMNH 51689, 51690, **Naturalis** RMNH 25906, **ZMB_Mam** 17518

Crossarchus obscurus MNHN 1962-1189, 2005-802, 2005-798, 2005-797, 2005-800, 1959-186, 1976-333, 1895-17, 1961-1027, 1931-44, 2001-2109, 1994-1302, 2004-628, 2000-1066, 2000-1070, 2000-1071, 2000-1063, 2000-1069, 2000-1067, 2000-1062, **Naturalis** RMNH 31322, RMNH 31323, ZMA 16502, ZMA 9852, RMNH 2639, SMF 16552, **ZMB_Mam** 45257, 44258, 44257, 82633, No_number_fem

Crossarchus platycephalus AMNH 241397, MNHN 1911-857, 2003-126, **ZMB_Mam** 82640, 8883, 82643, 82647, 82619, 82632a, 82632?, 82646, 82628, 82609, 82602, 82601, 82600, 82597, 82610 oder 621, 82613, 82615, 8884, 82642, 82624, 82638, 82612, 82626, 82618, 82605, 82639, 82614, 82635, 82636, 82780/82673, 82672, 82641, 14575, Dummy 2177? (2), No_number_ohne_Angaben, 8589

Cryptoprocta ferox AMNH 188213, MNHN A.12.208, 1974-148, 1927-227, 1977-554, 192 - 1668, 1940-1211, 1933-31, 1932-3553, 1880-2544, 1927-2366, 1977-556, 1977-555, 1992-1667, 1963-348, **Naturalis** RMNH 34453, RMNH 34451, RMNH 34452, RMNH 34454, ZMA 415, **NMP** 47070, 50467, 50457, 50466, 50444, 90184, SMF 6212, **UMZC** 8149, 5147, **ZFMK** 594, **ZMB_Mam** 27738, 90369, 4360, 5425

Cryptoprocta spelaea MNHN 1977-755, 1977-756

Cynictis penicillata AMNH 42948, 81757, 81755, 54096, 70390, 54095, 169014, 169016, 169017, 169018, 169019, 169020, 169021, 70415, 165754, 169022, **NMW** 18197, 18198, 18201, 18189, 18191, 18192, 18194, 18196, 18182, 18183, 18185, 18186, 18187, 18188, 18209, 18210, 18211, 18212, 18213, 18214, 18215, **ZFMK** 996, 994, 995, **ZMB_Mam** 21561, 21570, 82683, 37518, 37517, 11860, 82681, Dummy 2188? (Reich 9 12 1896), 21567, 82682, 32097

Cynogale bennetti AMNH 173509, **ZMB_Mam** 83041

Diplogale hosei **Naturalis** RMNH 34568

Dologale dybowskii AMNH 51018, 51608

Eupleres goudotii AMNH 100484, 880 - C.A., 100461, 188211, MNHN 1880-2540, 1962-2091, 1962-1121, 1880-2539, 1961-1029, 1962-1602, 1962-2105, SMF 34729, **ZMB_Mam** 4032, 4031, 44572, 43127, 60592, 4691

Felis bieti MNHN 1893-151

Felis catus AMNH 96295, 96294, 41557, 5369, 24416, 99978, 35072, 163028, 35073, 100339, 247045, 133972, 22818, 15977, 147174, 70280, 80212, **MNRJ** 615, 623, 3144, 0 - SM - Furos, 0 - SM - SF, 612, 0-M, **MZUSP** 22441, 43, 21618, 19903 **ZMB_Mam** Mummy 1, Mummy 3, Mummy 5, Mummy 6, Mummy 9, Mummy 10, Mummy 12, Mummy 14, Mummy 20, Mummy 21, Mummy 23, Mummy 28, Mummy 29, Mummy 32, Mummy 33, Mummy 34, Mummy 38, Mummy 40, Mummy 41, Mummy 42, Mummy 43, Mummy 44, Mummy 45, Mummy 47

Felis chaus AMNH 171166, 184683, 238649

Felis margarita SMF 38557, 38556, 38333, 38326, 44815, 44750, 40531, 51233, 50171, 47692, 47691, 53516, 53593, 53592, 53591, 53594, 53599, 53600, 53601, 53602, 53603, 53604, 53605, 55542, 55531, 55527, 55311, 54509, 53615, 53610, 55543, 55532, 55528, 55523, 54510, 53607, 55544, 55533, 55529, 55525, 55309, 53617, 53608, 55545, 55541, 55530, 55526, 55310, 54507

Felis nigripes AMNH 214380, **ZMB_Mam** 31704

Felis silvestris **NMP** 22156, 46746, 46753, 46754, 22686, 46752, 10035-3085 (1 - gelb), 10035-3085 (2 - weiss), 47550, 47553, 46916, 22742, **ZMB_Mam** 24806, 24807, 24803, 18478, 19153, 24803 (2), 18472, 94190, 18476, 18474 (silvestris), 62744, 17355, 18471, 94196, 8918, 7965, 8917, 70395, 25743, 91520, 22443, 19152, 28656, 20494, 94188, 45110, 45116, 45124, 45117, 70394, 45114, 12174, 22468, 45121, 1251, 45124 (2), 1249

Felis silvestris (lybica) AMNH 169457, 80893, 169458, **NMP** 48196, **ZMB_Mam** 41168, 62741, 29598, 29601, 8219 (A 622), 28567, 62739, 62743, 62738, 62733

Fossa fossana AMNH 188209, 100454, MNHN 1932-3555, 1962-2073, 1872-276, 2006-568, 1882-1594, 1962-1597, 1882-1589, 1932-3557, 1932-3556, 1962-2112, 1882-1590, 1962-1598, 1962-1599, 1882-1586, 1882-1592, **Naturalis** RMNH 34456, RMNH 34457, SMF 34841, **ZMB_Mam** 4862, 44575, 44576, 19723, 4822

Galerella ochracea **ZMB_Mam** A155.07 (another number not on skull?)

Galerella pulverulenta AMNH 161609, 161608

Galerella sanguinea central AMNH 82765, 82766, 83241, 83243, 83239, 83219, 83217, 83211, 83210, 83208, 83207, 83162, MNHN 2000-1072, 2000-1059, 1858-179, 1974-321, 1961-119, 1961-120, 1961-118, 2001-2188, 1875-286, 1982-213, 1902-533, 2000-1054, 1996-1540, 1939-195, 1918-17B (2 ligne), 1875-287, ZMB_Mam 61007, 26013 (kiste 21321), An 26020, 96916, A4392 / 14392, 40493, 21341, 20286

Galerella sanguinea south AMNH 169046, 169047, 169049, 169050, 169051, 169443, 161031, 161032, 87692, 81485, 81484, 81489, 81490, 86500

Galidia elegans AMNH 100473, 100466, 100465, 100469, 100472, MNHN 1961-973, 1962-2069, 1962-2071, 1932=3534, 1961-972, 1983-794, 1912-124, 1932-3527, 1882-1609, 1876-931, 1962-2089, 1962-2067, 1932-3529, 1893-468, 1992-1677, 1962-2070, 1932-3528, 1962-2066, 1992-1680, 1880-2552, 1962-1744, 1907-98, 2005-850, 1932-3530, 1962-2068, 1951-2, 1998-1938, 1962-2109, 1974-316, 1992-1685, Naturalis RMNH 34439, RMNH 34438, RMNH 34441, RMNH 34430, NMP 10789, SMF 34733, 2632, ZMB_Mam 83038, 44600, 16203, 4109

Galidictis fasciata AMNH 100479, MNHN 1882-1613, 1880-1962, 1932-3531, 1932-3539, 1882-1615, Naturalis RMNH 34436, ZMB_Mam 4111, 43126, 60469, 4112

Genetta abyssinica ZMB_Mam 1097

Genetta angolensis AMNH 89205, 89831

Genetta boursloni MNHN 2003-436, 2003-426

Genetta cristata ZMB_Mam 18975

Genetta felina ZMB_Mam 19739, 19740, 41442

Genetta genetta ZMB_Mam 18865, 18854, 18894, 18896, 44061, 44060, 44059, 44064, 44063, 44062, 44065, 42653, 15932, 41415, 42710, 42665, 42659, 42700, 41416, 42658, 41417, 42660, 41419, 42654, 41418, 42655, 42663, 42766, 42662, 42712, 42664, 41426, 40832, 42775, 42656, 42764, 42767, 41414, 42763, 42666, 42657, 42661, 42670, 42711, 42669, 42765, 41420, 19777, 18884, 18885, 18893, 68989, 44820, 18888, 18890, 12462, 19036

Genetta johnstoni MNHN 1986-246, 1982-1007

Genetta letabae ZMB_Mam 19677, 19679, 19864, 19863

Genetta maculata ZMB_Mam 19262, 19472, 19244 (maculata), 19204, 19230, 19388, 19251, 19187, 19412, 19202, 19310, 19399, 19236, 19482, 19390, 19478, 19288, 19311, 19397, 19325, 19260, 19313, 19486, 19322, 19181, 19212, 19474, 19484, 19480, 19238, 19634, 19210, 19200, 19261, 19523, 19536, 12225, 12226, 60969, 60968, 41498, 12596, 41405, 18923, 18922, 32463, 18879, 19417, 19003, 18977, 18126, 19054, 13373, 19407, 19289, 19458, 43648, 19460, 19862

Genetta pardina MNHN 1977-704, ZMB_Mam 18425, 1109

Genetta poensis ZMB_Mam 59101, 6407

Genetta schoutedeni ZMB_Mam 41780, 19032, 19024, 18909, 19232

Genetta servalina AMNH 51559, 170378, 119902, 36020, 51552, 51556, 51558, 51560, 51554, 51555, 36014, 36015, 36016, 36017, MNHN 1983-015, 1962-991, 1939-174, 1885-840, 1983-093, 1892-1211, Naturalis ZMA 18291, ZMA 9884, ZMA 18300, ZMA 18286, ZMA 18295, RMNH 2152, ZMA 18285, ZMA 18288, ZMA 18298, ZMA 18293, ZMA 9885, ZMB_Mam 18978, 18976, 18966, 18989, 19051, 18981, 18319, 18953, 18992, 18965, 18951, 19244 (2), 19045

Genetta thierryi ZMB_Mam 19041, 18128

Genetta tigrina AMNH 169060, ZMB_Mam 47066, 19681, 1102, 19661

Genetta victoriae AMNH 51411, 51420

Helogale hirtula AMNH 179094, 179109

Helogale parvula MNHN 1911-569, 1987-176, 1962-327, 1969-72, 1969-73, Naturalis RMNH 22950, RMNH 22949, RMNH 25808, SMF 89951, 44386, ZMB_Mam 40492, 18094, 27069, 27067, 38662, 9454, 6715, 19704, 18168, 7599, 18156, 17215, 22986, 7600, 10213, 27071, 13154, 25975, 22938, 26401, 18098, 18164, 18166, 10212, 9017, 12058, 5339, 22989, 22988, Dummy 2193, Dummy 2191, Dummy 2192, Dummy 2194, Dummy 2195, Dummy 2199, 38661, 22290, 78209, 3734, 1127

Hemigalus derbyanus AMNH 106006, 106625, 106005, 102450, 106064, 106774, 32658, MNHN 1886-24, 1871-554, 1877-195, 1962-1603, 404, 1897-1319, Naturalis RMNH 5109, RMNH 33699, geen Nummer - bij 33700, RMNH 34643, RMNH 33696, RMNH 33698, RMNH 33697, RMNH 33695, SMF 95197, 39243, UMZC 4481, ZFMK 277, 190, 554, ZMB_Mam 46442, 1096, 44018, 83200, 14294, 83208

Herpestes ichneumon AMNH 51590, 51588

Hyaena hyaena AMNH 64448, ZMB_Mam 82352, 14829, 14826, 82341, 82358, 82294, 82342, 82357, 16336, 82353, 42760, 11068, 16384, 16689, 14883, 45066, 39312, Dummy 2337? (A2732), 2733, 82336, 82345, 82302, 60974, 82304, 82359, 82343, 11717, 82349, 82296, 82329, 82300,

82332, 82340, AZ 3240?, 14342, 82348, 60978, 60975, 82350, 82303, 82305, 82308, 82355, 82356, 82360, 82301, 13251, 82362, 82337, 12655

Ichneumia albicauda **ZMB_Mam** 82754, 82744

Leopardus colocolo **AMNH** 76150, 189394, 243110, 133977, 16695, **MNHN** 1909-437, **MNRJ** 24911, **MZUSP** 7786, 13671, TX050631, TX040006

Leopardus geoffroyi **AMNH** 39010, 39004, 41553, 800298, 205907, 205910, 205911, 16696, 205909, 205905, 205914, 205904, 205906, 205903, 205908, 205913, **MNHN** 1962-2923, 1935-356, 1912-748, 3457, **MZUSP** 1443, 1432, 110, 111, **Naturalis** ZMA 11663, ZMA 9678, ZMA 2366, ZMA 17201, ZMA 12511, ZMA 21415, **NMP** 46496, **NMW** 3161, /B 2370, B 2267, **SMF** 65188, 63764, 60075, 60071, 55540, 47626, **ZMB_Mam** 7179, 1227, 105202, 105203, 105204, 105205, 7906

Leopardus guigna **AMNH** 933237, 33283

Leopardus guttulus **MNRJ** 5885, 49356, 3133, 7261, 25650, 74386, 79465, 610, 25651, 25726, 0, 0-B, 0-C, **MZUSP** 6549, 6459, 1393, 3799, 1395, 1878, 2810, 6262, 2362, 2320, 1168, 810, 2971, 13796, 2321, 3811, 6728, 401, 22416, 22415, 22417, 396, 13602, 11819, 32633, TX040001, TX050665, 1765, **ZMB_Mam** 21290, 46451

Leopardus mitis **MNRJ** 5679, 48894, 74382, 72786, 25691, 79122, 4812, 4811, 48877, 622, 624, 625, 7630, 24875, 24884, 24880, 24882, 24883, 48872, 48873, 48874, 48875, 48876, 48878, 48879, 71609, 0 - CB187, **MZUSP** 11472, 13595, 8633, 5553, 20427, 3069, 2643, 2638, 2639, 3070, 2733, 3113, 4239, 4238, 13673, 8879, 2964, 2963, 2913, 2914, 2839, 6277, 22447, 9414, 9423, 1805, 1936, 2966, 2962, 1167, 9422, 2968, 2967, 10354, 9615, 2931, 1241, 2467, 2465, 1937, 440, 3336, 9012, 7027, **SMF** 15719

Leopardus pardalis **AMNH** 145641, 272940

Leopardus pardinoides **AMNH** 69165, 69166

Leopardus tigrinus **MNRJ** 24894, 24896, 49354, 0-5145, **MZUSP** 21613, 2646, 19900, 32283

Leopardus wiedii **MNRJ** 5114, 4816, 6084, 25725, 24910, 72785, 79051, 5621, 24886, 24887, 24890, 0-5508, 0-B, **MZUSP** 1648, 5560, 5561, 5562, 3503, 2644, 2242, 2654, 28311, 9998, 6646, 2915, 19906, 10426, 2840, 2686, 2969, 1396, 467, 468, 1169, 2901, 1764, 40, 1398, 1397, 1400, 2029, 1649, 2030, 22414, 34, **ZMB_Mam** 21219, 21156, 21150, 21239, 44076

Leptailurus serval **MZUSP** 32391, **NMP** 50433, 46329, 94770, **ZMB_Mam** 13313, 13449, 58027, 58028, 58032, 57838, 57858, 58031, 58030, 20229 / 20230, 58034, 57865, 57853, 57855, 57849, 58036, 58037, 21046, 58039, 58064, 58041, 57856, 58052, 58051, 57861, 58047, 58050, 58045, 58044, 58048, 58055, 58061, 58060, 58059, 58056, 58057, 58054, 58058, 57864, 57851, 58067, 58065, 58066, 11914, 12264, 58069, 15607 (2)

Lynx canadensis **AMNH** 239831, 239833, **MNRJ** 49353

Lynx lynx **ZMB_Mam** 11973, 94201, 48693, 14589, 43640, 59097, 94202, 34052, 1272, 14375, 95541, 46447, 94200, 14344, 57998, 94203, 90803, 16997, 28796, 14549, 58002, 1273, 14857, 57999, 11178, 16624, 94199, 57786, 28684, 94204, 14852, 58000, 57997, 94198, 94197, 57787, 14854, "N 1331", 57996, 23036, 14855, Dummy 2013 (f384?), 3437, 6913, 7245 (1), 13177, 20462, N. 11, N. 1370, 4311 maybe

Lynx pardinus **AMNH** 169492, **ZMB_Mam** 58018

Lynx rufus **AMNH** 24066, 24665, 24668, 24666, 24664, 138408, 31766, 31767, 121282, 144935, 144930, 144933, 144932, 31765, 144929, 144937, 144931, 8063/6420, **MNHN** 2004-303, 1997-445, 1922-152, 1997-446, **MNRJ** 49355, **NMP** 47438, 94282, **ZMB_Mam** 58013, 12352, 58012, 58128, 1267, 12330 (1), 14858, 57800, 58016, 58015, 57802, 58017, 57801, 57805, 58014, 57803, 57812, 32412, A3968, 9186, 15992

Macrogalidia musschenbroekii **Naturalis** RMNH 32244, ZMA 629

Mungos gambianus **MNHN** 1950-265, 1981-555, **ZMB_Mam** 82670

Mungos mungo **MNHN** 2005-865, 1962-2078, 1886-865, 1897-636, 1911-2304, 1892-2059, 1902-530, 1939-192, **NMW** 2207, B2212, 82214, B5594, 1182, 1253, 62700, 68142, 68118, 1176, 1178, **ZMB_Mam** 60988, 16999, 20298, 7954, 82630, 82673, 82674, 82651, 82668, 20638, 82666, 82667, 82648, 82649, 34891 (?), 20639, 82661, 82662, 2908, 60987, 82656, 41983, 1131, 82663, 13476, 1081, 82658, dummy 2261?, "An 10094", dummy 2275, 70626, 70726, 18124, 18125, Dummy 2168, Dummy 2177?, Dummy 2167, 32405, 42551, Dummy 2170? (A4298), 12543, A2778, 21268

Mungotictis decemlineata **MNHN** 1992-1670, 1964-236

Nandinia binotata **AMNH** 51469, 51460, 51457, 51461, 51474, 51487, 51478, 51475, 51482, 51491, 51495, 51500, 51501, 51497, 51505, 51506, 51507, 51509, 51512, 51504, 51508, 51479, 51717, **ZMB_Mam** 48401, 1169, 18108, 1170, 82566, 30374, 82588, 82584, 16314, 18317, 82591, 44263, 16366, 82595, Dummy 2473 or 2474, 82567, 82564, 82592, Dummy 2473 or 2474

(2), 82560-82576 oder 82577A 60.05, 82560-82576 oder 82577A 60.05 (keiner), 12278, 82593, Dummy 2486, Dummy 2492 (225?), 20634

Neofelis diardi AMNH 19383, 35273, 35808, 22916, MNHN 1879-2133, **Naturalis** RMNH no number (Box 115-35), Buitenzorg 71/41 (box 115-35), RMNH no number Exp Snelleman 1878, RMNH 1784, RMNH 1780, RMNH 4717, ZMA 9413, ZMA 9412, ZMA 24455, ZMA 9478, RMNH no number box BE 109467, ZMA 21144, ZMA 13534, ZMA (?) 1975, **NMP** 46090, 46703, 46216, 48197, 46466, 46704, 46091, **NMW** 2793, 1477, 31066, 1380, **SMF** 15470, 51593, **ZFMK** 65-2, **ZMB_Mam** 52811, 22198, an1212, 22842, 56310, 22153, 50748

Neofelis nebulosa AMNH 238650, MNHN 1960-3663, 1961-217, 1961-101, 1971-86, **Naturalis** ZMA 577, **NMP** 46702, 46403, **NMW** 25125, **SMF** 73356, 40450, **ZFMK** 93-689, 76-378, 84-337, **ZMB_Mam** 33162, 81359, 47688

Otolobus manul AMNH 180268, MNHN 2010-646

Paguma larvata AMNH 184548, 184970, 184968, 184549, 184969, 103743, 103989, 45337, 106060, 106772, 163604, 106616, 106618, 57064, 57049, 43131, 43138, 84405, 84408, 85041, 87383, 35459, 1625, 43136, 84895, 114559, 119485, MNHN 1974-489, 1988-163, 1962-1588, 1962-2062, **ZMB_Mam** 13161, 83050, 43456, 36596, 43457, 36595, 11493, 13060, 11494, 83054, 83055, 26501, 83058, 83059, 83061, 83060, Dummy 2749, 83056, 1168 (2)

Panthera leo MNRJ 48867, 48866, 1024, 388, 1011, 1006, **MZUSP** TX050250, **UMZC** 5475, 5473, 5472, 5467.3, 5467.2, 5467, **ZMB_Mam** 55273, 55265, 55263, 55247, 34263, 28557, 28555, 20995, 55250, 55258, 55269, 55264, 55261, 35037, 33924, 15960, 20218, 20216, 55249, 55251, 55350, 55312, 55340, 55308, 55336, 55299, 55325, 55295, 55316, 55289, 55313, 55285, 55292, 55296, 55304, 55309

Panthera onca MNHN 1979-52, MNRJ 3349, 1023, 1021, 1017, 1007, 1027, 77863, 69170, 71161, 6021, 24860, 634, 1015, 32705, 1013, 633, 24862, 13508, 48871, 24861, 48869, 48868, 48870, 36218, 25687, **MZUSP** 13600, 13599, 19853, 2332, 11844, 3330, 11843, 21606, 3331, 469, 3420, 7161, 6806, 3752, 3685, 11469, 17550, 22452, 3686, Jirau 09012010b, Araguaia Silveira 2010, 28869, 2330, 2551, 265, Teles_pires, TX060397, 654

Panthera pardus MNHN 2006-436, **Naturalis** ZMA 76?, RMNH 1926, ZMA 267 (?? Only 267 on skull), **UMZC** 5821, **ZMB_Mam** 56357, 19892, 56330, 56329, 56469, 56457, 56471, 56475, 56476, 56472, 56478, 56466, 56460, 56477, 56464, 56459, 56338, 56502, 56474, 45068, 66666, 45070, 45069, 13453, 48215, 56420, 56413, 56480, 56365, 56424, 23428, 23427, 91299, 23429, 56379, 14480, 29473, 56384, 56387, 13705, 56408, 45071, 56411, 56388, 5560, 5559, Keine Nummer (aus dem aufgelösten Praktikumsschrank)

Panthera tigris MNRJ 70234, **MZUSP** TX050706, 050249 - 9158, **NMP** 46709, 47673, 46504, 46400, 50420, 46402, 46401, **ZMB_Mam** 13138, 12413, 7614, 7620, 22150, 56036, 56041, 56039, 56037, 56040, 56038, 28793, 42547, 52482, 52574, 2.12/2 eventuell zu 56026-56028-56029, 14366, 14367, 14369, 14368, 14370, 15640, 28794, 14365, 14364, 87040, 68380, 66394, 56049, 56044, 56045, 56048, 105216, 56043, 87036, Ohne nummer - 657?, 28792

Panthera uncia AMNH 35476, 166952, 207704, 119662, 35303, 24215, 35360, 35529, MNHN 1998-1248, 1970-102, 2006-429, A14597, **Naturalis** ZMA 12871, ZMA 11914, ZMA 8853, ZMA 2279, RMNH 12495, ZMA 5097, ZMA 8112, ZMA 4196, ZMA 11656, ZMA 8655, **NMP** 46750, 46467, 10790, 46404, 46405, 46725, 47005, **NMW** 6037, 11920, **SMF** 5870, 5419, **ZMB_Mam** 18434, 56313, 15839, 56312, 105239, 56314, 47690, 50810, 14501, 43160, 44022, 28560, 14598

Paracynictis selousi AMNH 116484, 116493

Paradoxurus hermaphroditus AMNH 240920, 150068, 59996, 113771

Paradoxurus musanga AMNH 102157, 102141, 107603, 102142, 107550, 107601, 101473, 101472, 101477, 101478, 101676, 101480, 101479, 101675, 101632, 102876, 102877, **ZMB_Mam** 83093, 83097, 42207, A3914 (which dummy), o.F which Dummy, 83074, 51800, 92126, 92128, 92127, 92130, 92074, 92263, 32403, 3433, 11950, II A 348, 70616, 34027, 60535, 83067, 83069, 83082, 83086, 83087, 83090, 91297, 91298, 40981, 40984, 42602, 42831

Paradoxurus philippinensis AMNH 103341, **ZMB_Mam** 6139, 2754, 5505

Paradoxurus zeylonensis MNHN 1876-2018

Parahyaena brunnea AMNH 81834, 83588, 83589, 83590, 169448, **ZMB_Mam** Dummy 2335 oder 2334, Dummy 2322 to Dummy 2330 - 1, Dummy 2322 to Dummy 2330 - 2 (II), 15809, A2734, 16810, Dummy 2333? - 1, 33685, Dummy 2333? - 2 (missing right canine), Dummy 2331, 18042, 18043, Dummy 2322 to Dummy 2330 - 3 (15), 82388, Dummy 2334 oder 2335 (Siehe 82370 auf Schädel geschrieben), Dummy 2321? (DSWA - Siehe 82372 und 82373 auf Schädel geschrieben), 82387, Dummy 2318? - B, 82386, 16808, Dummy 2318? - A (siehe Fell 82374 /76 auf Zettel geschrieben), 16811, 82384, 82383, 18041, 23426, Dummy 2318 - C (subadult), 11506, 82385, 41733, 31819, Dummy 2322 to Dummy 2330 - 4 (5 unterm Schädel geschrieben), Dummy 2322 to

Dummy 2330 - 5 (10 unterm Schädel geschrieben), Dummy 2322 to Dummy 2330 - 6 (12 unterm Schädel geschrieben), Dummy 2333? - 3, Dummy 2319, Dummy 2322 to Dummy 2330 - 7 (14 unterm Schädel geschrieben), Dummy 2322 to Dummy 2330 - 8 (13 unterm Schädel geschrieben), Dummy 2322 to Dummy 2330 - 9 (3 unterm Schädel geschrieben), Dummy 2322 to Dummy 2330 - 10 (7 unterm Schädel geschrieben), Dummy 2322 to Dummy 2330 - 11 (5 unterm Schädel geschrieben), Dummy 2322 to Dummy 2330 - 12 (6 unterm Schädel geschrieben), Dummy 2320

Poiana richardsonii AMNH 51439, 51438, 236587, MNHN 1976-389, *Naturalis* ZMA 15354, ZFMK 109, 110, 458

Prionailurus bengalensis NMP 46613, 47682, SMF 15720, 56155, 61195, 63771, 15718, 36412, 52489, 60058, 60262, 71753, ZIH48, 5788, 16248, 51591, 60057, 60680, 65183, 51235, 60648, 65182, 65186, 71755, ZMB_Mam 57987, 48634, 43143, 40636, 42591, 43144, 43145, 43142, 43146, 42593, 6363, 105222, 43462, 18474 (bengalensis), 36599, 57961, 11194, 43463, 16109, 14643, 70422, 13123, 57960, 31245, 34046, 14877

Prionailurus bengalensis x Felis catus SMF 51236, 81006

Prionailurus planiceps AMNH 173515, MNHN 1873-228

Prionailurus rubiginosus MNHN 1872-70, ZMB_Mam 5183

Prionailurus viverrinus AMNH 101627, 1021817, ZMB_Mam 43250, 44772, 44236, 15580, 16292, 13726, 13522, 11888, 12710, 13056 (2)

Prionodon linsang MNHN 1876-215, *Naturalis* RMNH 34764, ZMA 9858, RMNH 33550, RMNH 9842, RMNH 34770, NMW 2171, 49881, ZMB_Mam 4113, 37764, 48081, 68984, 48089

Prionodon pardicolor AMNH 163595, MNHN 1896-2065, 1929-424, *Naturalis* ZMA 24711, SMF 16517, ZMB_Mam 45381, 105410

Proteles cristata AMNH 169445, 165120, 173512, 88383, 169446, 169091, 114197, 34266, 169089, 81044, 27768, *Naturalis* RMNH 17276, RMNH 35120, RMNH 25893, RMNH 35125, RMNH 16898, RMNH 35126, ZMA 6467, ZMA 18697, NMW 1524, 1753, 1268, 64960, SMF 26741, 82180, 21342, 15693, 10134, UMZC 4010, 4001, 4002, ZFMK 62.36, 62.1, ZMB_Mam 39659, 7098 (2), Dummy 2360? (An 8772), 39657, 104316, 56793, 89495, 45001, 39656, 39658, 40754

Puma concolor MNRJ 381, 53862, 6022, 6023, 71077, 380, 985, 1014, 1016, 1018, 1019, 1025, 1020, 1026, 1028, 1029, 24867, 24868, 24869, 49074, 49075, MZUSP 32194, 1637, 19854, 2687, 3801, 20935, 11470, 9010, 9418, 9637, 10467, 10352, 9425, 9811, 17565, 11471, 28868, 32286, 7343, 3334, Jirau 09012010, 2385, ZMB_Mam 56118, 6470, 1210, 35811, 35810, 14847, 56116

Puma yagouaroundi MNHN 2006-545, 1913-16, 2001-1292, 1956-711, 1966-7, MNRJ 24885, 3140, 3153, 24901, 1039, 79490, 25724, 33513, 79049, 79444, 384, 49316, 1381, 49076, 0-CB72, MZUSP 13607, 5175, 5176, 13598, 13481, 3692, 2441, 2978, 2977, 3800, 1272, 7351, 2647, 7388, 37, 1003, 1647, 1399, 2031, 7203, 31985, TX050340, ZMB_Mam 21309, 46448, 21295, 5816, 5815

Rhynchogale melleri MNHN 1962-992, 1902-531

Salanoia concolor AMNH 100475, MNHN 1880-2554, 1866-233, 1962-325, 1880-2553, 1961-974, 1882-1611, 1962-2110, 1962-2107, 1962-2111, 1962-2108, *Naturalis* RMNH 34447, ZMB_Mam 16502, 5821, 8455, 13479, 43125

Smilodon populator UMZC 5413

Suricata suricatta AMNH 169452, 169454, 169451, 169453, 35637, 31277, 90441, 83645, 83646, 168990, 168991, 12, 168996, 168997, 169000, 169003, 169004, 161605, 161606, 161604, 168994, 161603, 169005, MNHN 1998-113, 1936-1534, MZUSP 13790, NMP 9782, NMW 66644, 57462, IR 215?, 22764, 63388, 1254, 401, 18330, 18326, 18327, 18328, 18329, ZMB_Mam 41443, 91343, 82680, 43168, 82782, 82781, 1054, 1054 (2), 70620, 82676

Urva auropunctata AMNH 60071, 27595, MNHN 2013-1935, 2013-1936

Urva brachyura AMNH 103988, ZMB_Mam 14295, 21092

Urva edwardsii AMNH 143029, 54525

Urva fusca AMNH 240856, ZMB_Mam 60534, 90742

Urva javanica AMNH 101656, 101492, 101491, 101490, 101495, 101653, 101493, 101494, 102030, 102029, 101733, 102031, 101658, 102221, 101657, 102913, 55556, MNHN 1982-107, 2000-133, 1962-2074, 1982-162, 1882-12, 1982-161, 1929-3379, 2004-621, 2004-622, *Naturalis* RMNH 33721, RMNH 33718, RMNH 22930, RMNH 20799, RMNH 33717, RMNH 33720, RMNH 33725, RMNH 34971, RMNH 33727, SMF 446, UMZC 4841, 4842, ZFMK 57.269, 65.3, 2000.001, ZMB_Mam 2907, 40977, 46120, 40979, 1134, 1135, 47540, 34040, 60544

Urva semitorquata AMNH 108803, 103746

Urva smithii AMNH 171168, 163188

Urva urva AMNH 112747, 60185, 112748, 60188, 112969, 113028, 163605, 276141, 184971, 185119, 43130, 60126, 185120, 185388, 184972, 184552, 184973, 84441, 45503, 59963, 60092, 60151, MNHN 1874-500, 1929-403, 1899-335, 1929-383, 1929-386, 1929-380, **Naturalis** RMNH 21024, RMNH 20857, RMNH 20855, RMNH 20856, ZMA 24714, **ZFMK** 82. 1, **ZMB_Mam** 21180, 21188, 21184, 21175, 47507, 43460, 46438, 21198, 21195, 36597
Urva vitticolla AMNH 240922, 163182
Viverra megaspila AMNH 31287
Viverra tangalunga AMNH 152878, 152880
Viverra zibetha AMNH 63766, 58381, 84344, 57056, 57055, 84346, 57054, 57052, 60175, 57053, 60141, 60094, 45512, 60140, 59316, 60179, 60178, 45505, 60177, 83985, 85045, 85046, 45510, 83443, 54781, 163593, 163594, 163592, 35450, 113482, 87367, 83435, MNHN 1994-2313, A-2091, 1877-703, A.3493, SMF 16516, 55777, 71748, 71749, ZMB_Mam 91053, 43453, 28554, 42610, 36594, 43452, 2753
Viverricula indica ZMB_Mam 40991, 42923, 42598, 42597, 40992, 40988, 40990, 40989, 40987, 11350, 68775, 68738, 42599, 60543, 43247, dummy_2821 (2820?), 68752, dummy_2820 (2821?), 68776, 68757, 68749, 68739, 68740, 37995, 43583, 3781, 43584, 43586, 1091, 68778, 68742, 68747, 5335, 59066, 42204, 43141, 11113, 13028, 68780, 68781, 68774, 68782, 68770, 68767, 37454, 36593, 68761, 68783, 43450, 31015, 14618, 13028 (2), 16466, Dummy 2823, 20534
Xenogale naso AMNH 51637, 51610

Appendix 2 - List of digitised specimens removed during outlier analysis.

Museum codes: **AMNH:** American Museum of Natural History (New York); **MNHN:** Muséum National d'Histoire Naturelle (Paris); **MNRJ:** *Museu Nacional da Universidade Federal do Rio de Janeiro*; **MZUSP:** *Museu de Zoologia da Universidade de São Paulo*; **Naturalis:** Naturalis Biodiversity Centre (Leiden); **NMP:** Přírodovědecké muzeum - Národní muzeum (Prague) **ZMB_Mam:** Museum für Naturkunde (Berlin). Specimen codes may not correspond to final registry numbers in some cases. Codes are as presented on skulls and/or on the boxes where they were stored, or include notes regarding the skull when a code was not present.

Acinonyx jubatus NMP 90449, 94688

Arctogalidia stigmatica Naturalis ZMA 1319

Cynictis penicillata ZMB_Mam 82684, Dummy 2188?

Felis catus ZMB_Mam Mummy 26

Galidia elegans AMNH 200878

Hemigalus derbyanus Naturalis RMNH 3478

Leopardus mitis MNRJ 79558

Panthera leo MZUSP 31979

Panthera tigris ZMB_Mam 12057

Paradoxurus musanga ZMB_Mam A 825 (dummy 2751 probably)

Parahyaena brunnea MZUSP 32353

Puma yagouaroundi MNHN 1962-1327, 1962-2955, 2000-359

Suricata suricatta MZUSP 13808, 13809

Viverra zibetha MNHN 1929-393

Viverricula indica MZUSP 19901

Appendix 3 - Extended Methods: Detailed description of methods for data acquisition and initial data management.

Landmark digitisation

Thirty-six (36) landmarks were recorded on each sampled specimen (12 on the sagittal line and 24 on both sides of the skull whenever possible) using a Microscribe MX (Immersion Corporation, San Jose, California) directly connected to a *laptop*; landmark coordinates were registered in the software Microsoft Excel. After the digitisation procedure all information were exported to the R programming environment.

Only adult or young adult were sampled, recognised based on teeth eruption and the suture closure levels. Specimens chosen for sampling had all landmarks preserved on at least one side of the skull (not necessarily all on the same side), except for the additional landmark CO (occipital condyle), not used for analyses in this work. This landmark was broken in a large number of specimens, and therefore was not registered for some digitised specimens. Whenever possible, we preferentially sampled specimens with sex and locality information available.

Twenty (20) of the landmarks registered were used for calculation of the linear distances between landmarks used as characters for all analyses (see below), which corresponded to those used by Porto *et al* (2009). The additional landmarks represent morphological variations possibly important for Carnivora, and may be used in future studies of the groups sampled. Most of these additional landmarks are shared with landmarks registered by a laboratory colleague working on Caniformians, which will allow comparability for future studies dealing with the order Carnivora as a whole. **Figure A3.1** shows the location and definition of all landmarks collected. The landmarks registered were considered homologous in all analysed groups, with the possible exception of landmarks PT and TSP, since large variations were present in some species at the boundaries between the frontal, parietal, squamosal and temporal bones. In attempting to keep these two landmarks as close as possible to their original definition, some species had individuals with these landmarks in their usual position (PT anterior to TSP), others in which both landmarks lay practically over one another, and others still in which PT shifted to a higher and more anterior position, lying dorsal to TSP. For these landmarks, therefore, homology may be only partial in some cases.

Prior to digitisation, skulls were fixed to a level surface using modelling clay or plastilin in two different views, allowing all landmarks to be reached. Landmarks in both view were later unified using a function that rotates landmarks on one view and unites corresponding landmarks. This procedure is described in greater detail below. Most individuals were digitised twice at least on one side of the skull, allowing an estimate of linear distance repeatabilities. When replicated measurements were taken from only one side of the skull, the replicate was always from the left side of the skull, since this side was less subject to errors due to difficulties in viewing and accessing landmarks. Almost all species with sample size equal or greater than 30 specimens had at least 30 individuals with replicated measurements. Only 6 species with $n \geq 30$ had less than 25 specimens with replicates: *Crocuta crocuta* (23 replicated specimens), *Lynx lynx* (22), *Panthera tigris* (15) and *Panthera pardus* (16), *Crossarchus obscurus* (15) and *Galerella sanguinea central* (20). Two species with lower sample sizes had few specimens with replicated measurements: *Arctogalidia trivirgata* (10) and *Prionailurus viverrinus* (2). The low number of replicates for *A. trivirgata* is a result of the recent division of traditionally recognised *A. trivirgata* in two species (*A. trivirgata* and *A. stigmatica* - Veron *et al*, 2015b). The relatively low number of replicates in *G. sanguinea central* similarly arises from a species division recognised after the sampling period (Rapson *et al*, 2012), while that for *C. obscurus* results from species reidentifications after sampling. Most digitised individuals was classified as *A. stigmatica* after an analysis for identification of specimens belonging to each of the two species, leaving *A. trivirgata* with low sample size and a small number of replicated measurements. For *Prionailurus viverrinus*, the low number of replicates (and relatively low sample size) is a result of the decision to digitise representatives of this species being taken at the end of the sampling period and prioritising the digitisation of a larger sample size for future analyses. Although the number of replicated measurements for *Prionailurus viverrinus* does not allow calculation of measurement repeatabilities, this species' morphology is relatively similar to that of *Prionailurus bengalensis* and other felids, and therefore measurement repeatability for this species is likely sufficiently well-represented by that calculated for these similar taxa.

Figure A3.1: Digitised Landmarks shown on a *Panthera onca* skull in dorsal, lateral and ventral views. *: landmarks used for calculation of the linear distances used in this work.

IS* - Medial point of the maxilla in the inferior tip of the septum between incisives; **NLE*** - Nasale, anterior suture between nasals; **NP** - Anteriormost lateral region of nasal bone; **PMP** - Posteriormost point of the premaxilla-maxilla suture; **FMN** - Anteriormost point of the frontal-maxilla suture, at the nasal border; **NON*** - Nasion, suture between nasal and frontal bones; **PFZ** - Frontal process of the zygomatic bone; **PZF** - Zygomatic process of the frontal bone; **BR*** - Bregma, suture between frontal and parietal bones; **LD*** - Lambda, suture between parietal and interparietal bones; **LD2** - "Lambda2", suture between interparietal and occipital bones; **ZS*** - Uppermost point of the zygomatic-maxilla suture; **ZYGS** - Anteriormost and uppermost point of the temporal-zygomatic suture; **ZI*** -

Lowermost and posteriormost point of the zygomatic-maxilla suture; **ZYGI*** - Posteriormost point of the temporal-zygomatic suture; **PT*** - Pterion, frontal-parietal-sphenoid suture; **TSP*** - Temporal-sphenoid-parietal suture; **AS*** - Asterion, junction between temporal-parietal and temporal-occipital sutures; **EAM*** - Anteriormost point of the external auditory meatus; **PEAM** - Posteriormost point of the external auditory meatus; **PBE** - Anteriormost point of the medial part of the presphenoid-basisphenoid suture; **BEO** - Anteriormost point of the medial part of the basisphenoid-basioccipital suture; **APET*** - Anteriormost point of the petrosal crest; **TS*** - Junction between the temporal-sphenoid suture and the tympanic bulla; **JP*** - Base of the jugular process, in the basioccipital-temporal suture; **CO** - Occipital condyle; **BA*** - Basion, ventral tip of the foramen magnum; **OPI*** - Opistion, dorsal tip of the foramen magnum; **PrM** - Anteriormost point of the premaxilla-maxilla suture in the sagittal plane; **MP** - Palatine-maxilla suture, in the sagittal plane; **PNS*** - Posteriormost point of the suture between the palatine bones; **CAA** - Anteriormost point of the alveolus of the last premolar tooth; **CAP** - Posteriormost point of the alveolus of the last premolar tooth; **MT*** - Point where the palatine-maxilla suture meets the palatine border. **PMA** - Anteriormost point of the premaxilla-maxilla suture/ Anteriormost point of the alveolus of the canine tooth; **PM*** - Junction between the premaxilla-maxilla suture and the alveolus of the canine tooth/ labialmost point of the alveolus of the canine tooth; **CP** - Posteriormost point of the alveolus of the canine tooth.

All digitised specimens were also photographed in dorsal, lateral and ventral views with the camera fixed to a tripod. These photos serve as a visual catalogue of specimens, and were sometimes used to verify landmark positions in specimens during

outlier analysis to distinguish individuals with actual distinctive morphologies from digitisation errors. The images may also be used in the future to obtain additional measurements. Mandibles of the specimens digitised were also photographed in lateral view whenever available, and may be used for future work on the same clades. Specimens were photographed alongside a ruler or another instrument allowing determination of their scale. In order to reduce parallax effects, specimens were preferentially positioned at the centre of the image and distant from the camera.

Sampling

Data collection resulted in a total of 2740 digitised specimens, and was carried out in 11 institutions: MZUSP: *Museu de Zoologia da Universidade de São Paulo*; MNRJ: *Museu Nacional da Universidade Federal do Rio de Janeiro*; AMNH: American Museum of Natural History (New York, USA); ZMB - *Museum für Naturkunde* (Berlin, Germany); ZFMK - *Zoologisches Forschungsmuseum Alexander Koenig* (Bonn, Germany); SMF - *Naturmuseum Senckenberg* (Frankfurt am Main, Germany); MNHN - *Muséum National d'Histoire Naturelle* (Paris, France); NMW - *Naturhistorisches Museum Wien* (Vienna, Austria); UMZC - University Museum of Zoology (Cambridge, England); Naturalis Biodiversity Centre (Leiden, Netherlands); NMP - *Přírodovědecké muzeum, Národní muzeum* (Prague, Czech Republic). The impossibility of collecting data at the Natural History Museum in London, due to a long project for renovation of the collections making it unavailable for visitation during practically the whole period of this work, has unfortunately reduced the sample size available for some rare species, and prevented digitisation of material for some taxa.

Sampling was primarily focused on species most likely to have sufficient sample sizes for covariance matrix estimation and which, at the same time, represented ample taxonomic coverage of Feliformia. For the last reason, we made an effort to obtain samples from taxa relatively rare in zoological collections, but phylogenetically distinct and often ignored in studies of Carnivorans, like *Prionodon* (the only representative of family Prionodontidae) and malagasy carnivores (family Eupleridae). Besides this primary focus, we also attempted to include small samples (at least one or two individuals, including both sexes whenever possible) for as many species/taxa as possible, in order to gather a representative dataset of Feliformia for future studies based on average morphology. Specimens measured for this purpose include two *Felis catus* x *Prionailurus bengalensis* hybrids and a single skull cast (based on an actual specimen)

of the extinct macharodontine felid *Smilodon populator*, from the University Museum of Zoology (Cambridge).

An extensive process of taxonomic verification and reidentification of specimens was performed during data collecting and processing. The final list of specimens sampled per species is therefore presented after the section discussing the taxonomic confirmation/reidentification procedure.

Unification of views

The landmark coordinates taken in both views were superimposed using a least-squares procedure using landmarks common to both views (Schönemann, 1966), in order to produce a single landmark configuration for each specimen. Shared landmarks used for this procedure were: IS, NLE, NON, BR and BA (midline), NP, PMP, FMN, PFZ, PZF, ZS, ZYGS, PT and TSP (on both sides of the skull), for a total of 23 shared landmarks. In some cases, some landmarks were digitised on only one side of the skull due to difficulties in reaching parts of the skull. In these cases, unification used the subset of landmarks effectively registered in both views. This is unlikely to have caused problems for the unification procedure, since the number of landmarks effectively used for unification was always considerably higher than the minimum of 3 landmarks required for superimposition.

The superimposition procedure involved finding a rotation matrix $\mathbf{R}$ which satisfied

$$\mathbf{A}_c = \mathbf{Z}_c \cdot \mathbf{R}$$

where $\mathbf{A}_c$ and $\mathbf{Z}_c$ are the centralised matrices of landmarks shared between views. According to Schönemann (1966), the solution which minimises the sum of squared distances between landmarks is

$$\mathbf{R} = \mathbf{V} \mathbf{D}^* \mathbf{U}$$

where $\mathbf{V}$ and $\mathbf{U}$ are obtained from singular value decomposition of the matrix $\mathbf{M}$, defined as

$$\mathbf{M} = \mathbf{A}_c^t \cdot \mathbf{Z}_c$$

as follows:

$$\mathbf{M} = \mathbf{U} \cdot \mathbf{D} \cdot \mathbf{V}.$$

Matrix $\mathbf{D}^*$ in turn is directly obtained from $\mathbf{D}$, so that

$$d_{ij}^* = \begin{cases} \frac{d_{ij}}{[d_{ij}]}, & \text{se } i = j \\ 0, & \text{se } i \neq j \end{cases}$$

where d_{ij}^* and d_{ij} are the elements of matrices $\mathbf{D}^*$ and $\mathbf{D}$, respectively. The complete configurations, including landmarks registered in both views, were obtained unifying matrices $\mathbf{A}$ and $\mathbf{Z}^*$, where

$$\mathbf{Z}^* = \mathbf{Z} \cdot \mathbf{R}_i$$

$\mathbf{A}$ and $\mathbf{Z}$ correspond to the landmarks taken in view "A" and "Z", respectively, with $\mathbf{A}$ and $\mathbf{Z}$ centralised on the landmarks shared between views. For the latter, the averages between $\mathbf{A}$ and $\mathbf{Z}$ after the superimposition were used as the final coordinates.

In some cases, digitisation errors were recognised on some landmarks shared between views, easily identified after superimposition due to distances between views larger than that found for most landmarks. In these cases, the original landmark configuration of each view was verified and compared to photographs of the specimens in question. In all cases, the digitisation errors were recognised as having occurred in one view only - usually for landmarks harder to reach in one of the views. By removing the registration of the landmark from the view presenting problems and re-running the superimposition procedure using the remaining shared landmarks, these specimens could be preserved in the final sample. This removal of landmark registration from one view left a number of shared landmarks much higher than the minimum of 3 for superimposition in all cases.

Obtaining symmetrical landmark configurations; fragmented skulls

Effects of asymmetry in the unified landmark configurations were removed using a technique similar to that used for unifying the views, but reflecting points on one side of the skull over those on the opposite side, as proposed in Klingenberg *et al* (2002). In this process, the rotation matrix $\mathbf{R}$ is estimated for

$$\mathbf{X}_e = \mathbf{O}_e \cdot \mathbf{R}_i$$

where $\mathbf{X}$ is the original landmark configuration and e

$$\mathbf{O} = \mathbf{Q} \cdot \mathbf{A}' \cdot \mathbf{X}_i$$

where $\mathbf{Q}$ is a permutation matrix which projects landmarks on one side of the skull to the opposite side and $\mathbf{A}'$ is a rotation matrix with determinant = -1 (Mardia *et al*, 2000). Thus, the matrix $\mathbf{O}$ is a mirror image of $\mathbf{X}$.

$\mathbf{X}_c$ and $\mathbf{O}_c$ are the shared (midline) landmarks, used to estimate the rotation matrix $\mathbf{R}$. Landmarks missing from one side of the skull in the original landmark configuration $\mathbf{X}$ can then be obtained as entries from matrix

$$\mathbf{O}^* = \mathbf{O} \cdot \mathbf{R},$$

since both matrices are centralised on the shared (midline) landmarks. This technique is similar to that used to reflect points on one side of a configuration to the opposite side using its midline (Mardia *et al*, 2000).

This procedure created complete hemicrania for specimens in which some landmarks used for calculating distances were preserved in different sides of the skull, thus allowing the use of these fragmented skulls for calculation of distances in the recomposed symmetrical skulls.

Calculation of linear measurements

Thirty-five (35) linear measurements were produced from 20 of the landmarks using the symmetrical configurations produced as described above. The distances used were the same employed by Porto *et al* (2009; 2013), and are described in **Table A3-1**

For each replicate of each specimen, distances between landmarks were produced from symmetrical skulls using the Pythagorean theorem:

$$dist_{AB} = \sqrt{(A_x - B_x)^2 + (A_y - B_y)^2 + (A_z - B_z)^2}.$$

As skull asymmetry was removed during the procedure described above, the distance calculated on both sides of the recomposed skull is necessarily identical, and therefore no further changes to the distances calculated are needed.

Table A3-1: Set of 35 linear measurements used as characters in this work (following Porto *et al*, 2009; 2013) and their respective skull regions.

Distance	Region	Distance	Region
IS-PM	Face	ZS-ZI	Face
IS-NLE	Face	ZI-MT	Face
IS-PNS	Face	ZI-ZYGI	Face
PM-ZS	Face	ZI-TSP	Face
PM-ZI	Face	MT-PNS	Face
PM-MT	Face	PNS-APET	Neurocranium
NLE-NON	Face	APET-BA	Neurocranium
NLE-ZS	Face	APET-TS	Neurocranium
NLE-ZI	Face	BA-EAM	Neurocranium
NON-BR	Neurocranium	EAM-ZYGI	Face
NON-PNS	Face	ZYGI-TSP	Face
BR-PT	Neurocranium	LD-AS	Neurocranium
BR-APET	Neurocranium	BR-LD	Neurocranium
PT-APET	Neurocranium	OPI-LD	Neurocranium
PT-BA	Neurocranium	PT-AS	Neurocranium
PT-EAM	Neurocranium	JP-AS	Neurocranium
PT-ZYGI	Face	BA-OPI	Neurocranium
	Face/		
PT-TSP	Neurocranium		

Taxonomy, species confirmation and reidentification

We used Wozencraft (2005)'s taxonomy as a basis for this work, but include various changes proposed in recent results in carnivore taxonomy and systematics. We consider Asian linsangs (*Prionodon*) as representatives of their own family, Prionodontidae, the sister group to Felidae, following Gaubert & Veron (2003), Barycka *et al* (2007), Eizirik *et al* (2010) and Nyakatura & Bininda-Emonds (2012). We use *Urva* as the valid name for Asian mongooses and *Xenogale naso* as the valid name for the long-nosed mongoose, keeping *H. ichmeumon* as the only representative of the genus *Herpestes* (Patou *et al*, 2009). Traditional *Galerella sanguinea* is considered to comprise two groups (*G. sanguinea central* and *south*) representing unnamed putative species from Central and East Africa and from Southern Africa, respectively, as proposed by Rapson *et al* (2012). *Galerella flavescens* and *G. nigrata* were considered

as possibly different species (following Rathbun & Cowley, 2008), although this did not influence the work since samples could not be obtained for these taxa. As recently suggested by Veron *et al*, 2015a, traditional *Arctogalidia trivirgata* is separated in two species (*Arctogalidia stigmatica* and *A. trivirgata*). Similarly, we follow Patou *et al* (2010) and Veron *et al* (2015b) in considering three separate species of Asian palm civets: *Paradoxurus hermaphroditus* (from India and western Indochina), *Paradoxurus phillipinensis* (Borneo, Phillipines and Mentawai Islands) and *Paradoxurus musanga* (eastern Indochina, Sumatra, Java and Lesser Sunda Islands). The putative genets *Genetta "letabae"* and *Genetta "schoutedeni"* proposed by Gaubert *et al* (2004a,c; 2005b,c) are considered as species. We follow Trigo *et al* (2013) in separating *Leopardus guttulus* from *L. tigrinus*, and also consider the Central American ocella (*L. pardinoides*) as distinct, following Nascimento (2010) and Li *et al* (2015). Ocelots are divided in *Leopardus pardalis* (from North and Central America) and *L. mitis*, as suggested by Nascimento (2010) and at least partially supported by Janečka *et al* (2007) and Ruiz-Garcia *et al* (2012). *Neofelis diardi* is considered distinct from *N. nebulosa*, following Wilting *et al* (2007) and Christiansen (2008). *Leopardus colocolo* includes *braccatus* and *pajeros*, as suggested by Eizirik *et al* (*submitted*), and *Felis silvestris* includes *F. lybica*, as proposed by Driscoll *et al* (2007). On the other hand, *Felis bieti* is kept as a separately species (which does not influence the analyses given the low sample size for this species). *Felis catus* is considered separate despite Driscoll *et al* (2007)'s results, in order to allow investigation of differences between wild and domesticated forms and due to differences in their social behaviour (Macdonald *et al*, 2000). *Salanoia durrelli* (Durbin *et al*, 2010) was considered as a distinct species from *S. concolor*, but *Eupleres goudotii major* was provisionally considered as a subspecies of *E. goudotii* despite Goodman & Helgen (2010)'s analysis. The latter two decisions also do not affect the analyses, since samples for *S. durrelli* and *E. g. major* could not be obtained.

The confirmation and at times correction of species identifications in museum tags was an important part of the work during the data collection stage. This procedure was particularly relevant for clades which recently underwent taxonomic revisions and/or had traditionally recognised species split into two or more new species, like *Genetta* (Gaubert *et al*, 2004 a,b, Gaubert *et al*, 2005a,b; see also Phillipe Gaubert's website dedicated to genets and ocelots/ African linsangs: <http://lis->

upmc.snv.jussieu.fr/xper2/bases.Html/genettes_en/web/index.html), *Paradoxurus* (Veron *et al*, 2014), *Herpestes/Urva/Xenogale* (Veron *et al*, 2004; Patou *et al*, 2009) and *Crossarchus* (Sonet *et al*, 2014). Other data sources were also used as guidelines for species identification; for African species in particular, Kingdom & Hoffman (2013)'s handbook was an important source of information on skull characters useful for species determination.

After calculating linear measurements for each specimen, additional analyses were carried out on certain groups of species in an attempt to recognise specimens with doubtful or possibly wrong species identification during the data collection stage. This procedure was important to confirm reidentifications done during data gathering, and also for groups of morphologically similar species, including: *Catopuma* (*badia* and *temminckii*); *Crossarchus* and *Mungos* (these genera are frequently confused and often had imprecise identifications in museum tags); *Felis*; *Galerella*; *Arctogalidia* (due to the recognition of a likely second species, *A. stigmatica*, after the end of the data collection stage); *Genetta*; *Herpestes/Urva/Xenogale*; *Hyaena/Parahyaena/Crocota*; *Lynx*; *Prionodon*; *Neofelis*; *Paradoxurus*; *Leopardus*; *Panthera* and *Viverra/Viverricula*.

The procedure used during this stage included different forms of analysis. Principal Component Analysis (PCA) of specimens in each group of species were used to assess the possibility of distinguishing between genera/species based on its results, and to identify specimens grouped with species different from its initial identification. Linear discriminant analysis (LDA) using genus and/or species as factors were used to distinguish species and/or groups which could not be properly differentiated with PCA and to reclassify specimens with doubtful identifications. Skull characteristics (linear distances and/or characters observable in the photographs taken during data collection) of specimens with doubtful or initially wrong were also compared to descriptions in the literature. In some cases, the final classification followed that indicated in previous works using the same specimens, especially works focused on taxonomy and systematics.

The considerable effort used to confirm identifications led to reidentification of 121 specimens. A list of specimens reidentified during data collection and data analysis, as well as some specimens with particular morphologies whose identification was kept, is provided in **Appendix 19**.

Outlier removal

After confirmation and changes in species identifications, the data for each species were analysed in order to identify and remove outliers representing possible digitisation errors.

Outlier identification (and only this process) used a procedure based on Procrustes superimposition of the 20 landmarks used for calculation of the linear measurements for all specimens of each species, followed by an analysis of the distribution of Procrustes distances between each individual and the species mean shape (i.e. square root of the squared distances between the specimen and the mean shape for each landmark), using the "plotOutliers" R function (package "geomorph" - Adams & Otárola-Castillo, 2013). Specimens with Procrustes distances above the upper quartile were considered as potential outliers and separated for more detailed analysis.

The landmark configuration of potential outliers was compared to the species' mean shape, and also to pictures of the specimen in question obtained during data gathering. In some cases, comparison with the pictures revealed that the configurations corresponded to the actual morphology of the specimens; in these cases, the specimens were kept in the sample. When analysis of the pictures showed noticeable differences between the landmark configuration for a specimen and the morphology seen in the pictures, and also when the morphology of a specimen was particularly unusual for its species, the specimens in question were removed from the sample. A total of 20 outliers were recognised in this way, keeping a total of 2720 specimens for all further analyses. Lists of the material used for analysis and the specimens removed from the sample are available on **Appendices 1** and **2**, respectively.

The distribution of linear measurements within each species after outlier removal are approximately bell-shaped for most characters. Distortions still existing in some characters, like effects of bi- or multimodality, disappeared in most cases after correction for external factors of variation (see **Appendix 5**). After this correction, deviations from normality (Lilliefors tests, $\alpha < 0.05$) were found for few characters (≤ 4 for most species, up to 7 for *Neofelis nebulosa*).

Total sample

After species reidentification and outlier removal, the total sample includes 2720 specimens representing 121 recent species/clades, one fossil species (*Smilodon populator*, 1 specimen), one subfossil (*Cryptoprocta spelaea*, 2 specimens) and a hybrid between two felid species (*Felis catus* x *Prionailurus bengalensis*, 2 specimens). The sample obtained constitutes a Feliformia database with large phylogenetic coverage, including over 90% of the species currently recognised. The total sample obtained per species/taxon is shown in **Table A3-2**, along with the total number of specimens with replicated measurements for each species.

Table A3-2: Sample size after outlier removal (n) and number of specimens with replicated measurements (nreps) per species.

Família	Espécie	nreps	n	Família	Espécie	nreps	N
Eupleridae	<i>Cryptoprocta ferox</i>	34	34	Eupleridae	<i>Cryptoprocta spelaea</i> ¹	2	2
	<i>Eupleres goudotii</i>	18	18		<i>Mungotictis decemlineata</i>	2	2
	<i>Fossa fossana</i>	25	25	Felidae	<i>Caracal aurata</i>	2	2
	<i>Galidia elegans</i>	37	46		<i>Catopuma badia</i>	1	1
	<i>Galidictis fasciata</i>	11	11		<i>Catopuma marmorata</i>	2	2
	<i>Salanoia concolor</i>	17	17		<i>Felis bieti</i>	1	1
Felidae	<i>Acinonyx jubatus</i>	30	48		<i>Felis chaus</i>	3	3
	<i>Caracal caracal</i>	30	50		<i>Felis nigripes</i>	2	2
	<i>Catopuma temminckii</i>	31	40		<i>Leopardus guigna</i>	2	2
	<i>Felis catus</i>	27	52		<i>Leopardus pardalis</i>	2	2
	<i>Felis margarita</i>	30	49		<i>Leopardus pardinoides</i>	2	2
	<i>Felis silvestris</i>	35	63		<i>Lynx canadensis</i>	3	3
	<i>Leopardus colocolo</i>	11	11		<i>Lynx pardinus</i>	2	2
	<i>Leopardus geoffroyi</i>	32	47		<i>Otocolobus manul</i>	2	2
	<i>Leopardus guttulus</i>	41	43		<i>Prionailurus bengalensis x Felis catus</i>	1	2
	<i>Leopardus mitis</i>	72	72		<i>Prionailurus planiceps</i>	2	2
	<i>Leopardus tigrinus</i>	8	8		<i>Prionailurus rubiginosus</i>	2	2
	<i>Leopardus wiedii</i>	45	50		<i>Smilodon populator</i> ¹	1	1
	<i>Leptailurus serval</i>	31	51	Herpestidae	<i>Bdeogale crassicauda</i>	2	2
	<i>Lynx lynx</i>	22	50		<i>Bdeogale jacksoni</i>	2	2
	<i>Lynx rufus</i>	30	46		<i>Bdeogale nigripes</i>	2	2
	<i>Neofelis diardi</i>	25	40		<i>Crossarchus alexandri</i>	4	4
	<i>Neofelis nebulosa</i>	14	17		<i>Dologale dybowskii</i>	2	2
	<i>Panthera leo</i>	28	49	Herpestidae	<i>Galerella ochracea</i>	1	1
Felidae	<i>Panthera onca</i>	54	54		<i>Galerella pulverulenta</i>	2	2
	<i>Panthera pardus</i>	17	52		<i>Helogale hirtula</i>	2	2
	<i>Panthera tigris</i>	15	47		<i>Herpestes ichneumon</i>	2	2
	<i>Panthera uncia</i>	29	46		<i>Ichneumia albicauda</i>	2	2
	<i>Prionailurus bengalensis</i>	30	50		<i>Mungos gambianus</i>	3	3
	<i>Prionailurus viverrinus</i>	2	12		<i>Paracynictis selousi</i>	2	2
	<i>Puma concolor</i>	43	50		<i>Rhynchogale melleri</i>	2	2

References

- Adams, D.C.; Otarola-Castillo, E. 2013. geomorph: an R package for the collection and analysis of geometric morphometrics shape data. *Methods in Ecology and Evolution* 4: 393-399.
- Barycka, E. 2007. Evolution and systematics of the feliform Carnivora. *Mammalian Biology* 72(5):157-282.
- Christiansen, P. 2008. Species distinction and evolutionary differences in the Clouded Leopard (*Neofelis nebulosa*) and Diard's Clouded Leopard (*Neofelis diardi*). *Journal of Mammalogy* 89(6): 1435-1446.
- Driscoll, C.A.; Menotti-Raymond, M.; Roca, A.L.; Hupe, K.; Johnston, W.E.; Geffen, E.; Harley, E.H.; Delibes, M.; Pontier, D.; Kitchener, A.C.; Yamaguchi, N.; O'Brien, S.J.; Macdonald, D.W. 2007. The Near Eastern Origin of Cat Domestication. *Science* 317: 519-523.
- Durbin, J.; Funk, S.M.; Hawkins, F.; Hills, D.M.; Jenkins, P.D.; Moncrieff, C.B.; Ralainasolo, F.B. 2010. Investigations into the status of a new taxon of *Salanoia* (Mammalia: Carnivora: Eupleridae) from the marshes of Lac Alaotra, Madagascar. *Systematics and Biodiversity* 8(3): 341-355.
- Eizirik, E.; Johnson, W.E.; O'Brien, S.J. in prep. Molecular systematics and revised classification of the family Felidae (Mammalia, Carnivora). *Journal of Mammalogy*. Disponível online no endereço:
<http://dobzhanskycenter.bio.spbu.ru/pdf/sjop/MS636%20Eizirik%20Felid%20Taxonomy.pdf>
- Eizirik, E.; Murphy, W.J.; Koepfli, K.-P.; Johnson, W.E.; Dragoo, J.W.; Wayne, R.K.; O'Brien, S.J. 2010. Pattern and timing of diversification of the mammalian order Carnivora inferred from multiple nuclear gene sequences. *Molecular Phylogenetics and Evolution* 56:49-63.
- Gaubert, P.; Aniskin, V.M.; Dunham, A.E.; Crémère, C.; Volobouev, V.T. 2004b. Karyotype of the rare Johnston's genet *Genetta johnstoni* (Viverridae) and a reassessment of chromosomal characterization among congeneric species. *Acta Theriologica* 49(4): 457-464.
- Gaubert, P.; Fernandes, C.A.; Bruford, M.W.; Veron, G. 2004a. Genets (Carnivora, Viverridae) in Africa: An evolutionary synthesis based on cytochrome b sequences and morphological characters. *Biological Journal of the Linnean Society* 81:589-610.
- Gaubert, P.; Taylor, P.J.; Fernandes, C.A.; Bruford, M.W.; Veron, G. 2005a. Patterns of cryptic hybridization revealed using an integrative approach: a case study on genets (Carnivora, Viverridae, *Genetta* spp.) from the southern African subregion. *Biological Journal of the Linnean Society* 86: 11-33.
- Gaubert, P.; Taylor, P.J.; Veron, G. 2005b. Integrative taxonomy and phylogenetic systematics of the genets (Carnivora, Viverridae, *Genetta*): A new classification of the most speciose carnivoran genus in Africa. In: *African Biodiversity: Molecules, Organisms Ecosystems. Proceedings of the 5th International Symposium on Tropical Biology*, Museum Koenig, Bonn. B.A.
- Huber, B.J.; Sinclair, K.H. Lampe (eds): 371-383.
- Gaubert, P.; Veron, G. 2003. Exhaustive sample set among Viverridae reveals the sister-group of felids: The *linsangs* as a case of extreme morphological convergence within Feliformia. *Proceedings of the Royal Society of London: Biological Sciences* 270:2523-2530.
- Goodman, S.M.; Helgen, K.M. 2010. Species limits and distribution of the Malagasy carnivoran genus *Eupleres* (Family Eupleridae). *Mammalia* 74: 177-185.
- Janečka, J.E.; Walker, C.W.; Tewes, M.E.; Caso, A.; Laack, L.L.; Honeycutt, R.L. 2007. Phylogenetic relationships of ocelot (*Leopardus pardalis albescens*) populations from the Tamaulipan Biotic Province and Implications for Recovery. *The Southwestern Naturalist* 52(1): 89-96.
- Kingdom, J.; Hoffman, M. 2013. *The Mammals of Africa V: Carnivores, Pangolins, Equids and Rhinoceroses*. Bloomsbury, London, UK. pp. 328-330.
- Klingenberg, C. P., Barluenga, M., e Meyer, A. 2002. Shape analysis of symmetric structures: quantifying variation among individuals and asymmetry. *Evolution* 56(10): 1909-1920
- Li, G.; Davis, B.W.; Eizirik, E.; Murphy, W.J. 2016. Phylogenomic evidence for ancient hybridization in the genomes of living cats (Felidae). *Genome Research* 26(1): 1-11. doi: 10.1101/gr.186668.114.
- Macdonald, D.W.; Yamaguchi, N.; Kerby, G. 2000. Group-living in the domestic cat: its sociobiology and epidemiology. In: *The Domestic Cat: The Biology of Its Behaviour*. Turner, D.C. Cambridge University Press. pp 95-118.
- Mardia, K., Bookstein, F. L., & Moreton, I. 2000. Statistical assessment of bilateral symmetry of shapes. *Biometrika* 87(2): 285-300
- Nascimento, F.O. 2010. Revisão taxonômica do gênero *Leopardus* Gray, 1842 (Carnivora, Felidae). Tese de Doutorado, Instituto de Biociências, Universidade de São Paulo.

- Nyakatura, K.; Bininda-Emonds, O.R.P. 2012. Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. *BMC Biology* 10(12): doi:10.1186/1741-7007-10-12
- Patou, M.-L.; Mclenachan, P.A.; Morley, C.G.; Couloux, A.; Jennings, A.P.; Veron, G. 2009. Molecular phylogeny of the Herpestidae (Mammalia, Carnivora) with a special emphasis on the Asian Herpestes. *Molecular Phylogenetics and Evolution* 53: 69-80.
- Patou, M.-L.; Wilting, A.; Gaubert, P.; Esselstyn, J.A.; Cruaud, C.; Jennings, A.P.; Fickel, J.; Veron, G. 2010. Evolutionary history of the *Paradoxurus* palm civets - a new model for Asian biogeography. *Journal of Biogeography* 37(11): 2077-2097.
- Porto, A.; Oliveira, F.B.; Shirai, L.T.; de Conto, V.; Marroig, G. 2009. The Evolution of Modularity in the Mammalian Skull I: Morphological Integration Patterns and Magnitudes. *Evolutionary Biology* 36:118-135.
- Porto, A.; Shirai, L.T.; Oliveira, F.B.; Marroig, G. 2013. Size variation, growth strategies and the evolution of modularity in the mammalian skull. *Evolution* 67(11): 3305-3322
- Rapson, S.A.; Goldizen, A.W.; Seddon, J.M. 2012. Species boundaries and possible hybridization between the black mongoose (*Galerella nigrata*) and the slender mongoose (*Galerella sanguinea*). *Molecular Phylogenetics and Evolution* 65: 831-839.
- Rapson, S.A.; Goldizen, A.W.; Seddon, J.M. 2012. Species boundaries and possible hybridization between the black mongoose (*Galerella nigrata*) and the slender mongoose (*Galerella sanguinea*). *Molecular Phylogenetics and Evolution* 65: 831-839.
- Rathbun, G.B.; Cowley, T.E. 2008. Behavioural ecology of the black mongoose (*Galerella nigrata*) in Namibia. *Mammalian biology* 73: 444-450.
- Ruiz-Garcia, M.; Corrales, C.; Pinedo-Castro, M. 2012. Craniometric and Microsatellite genetic differentiation among putative ocelot subspecies (*Leopardus pardalis*) throughout Latin America. In: *Molecular Population Genetics, Phylogenetics, Evolutionary Biology and Conservation of the Neotropical Carnivores*. Ruiz-Garcia, M.; Shostell, J. (eds). Nova Science Publishers, Inc., New York (USA).
- Schönemann, P. 1966. A generalized solution of the orthogonal procrustes problem. *Psychometrika*, 31(1):1-10
- Sonet, G.; Colyn, M.; Verheyen, E.; Nagy, Z.T.; Wendelen, W.; van Rompaey, H.; Hulselmans, J. 2014. Afrotropical forest-dwelling mongooses (Mammalia: Herpestidae: *Crossarchus*) investigated by craniometry and mitochondrial DNA. *Journal Zool Syst and Evol Research*: doi: 10.1111/jzs.12066.
- Trigo, T.C.; Schneider, A.; Oliveira, T.G.; Lehugeur, L.M.; Silveira, L.; Freitas, T.R.O.; Eizrik, E. 2013. Molecular Data Reveal Complex Hybridization and a Cryptic Species of Neotropical Wild Cat. *Current Biology* 23: 1-6.
- Veron, G.; Colyn, M.; Dunham, A.E.; Taylor, P.; Gaubert, P. 2004. Molecular systematics and origin of sociality in mongooses (Herpestidae, Carnivora). *Molecular Phylogenetics and Evolution* 30: 582-598.
- Veron, G.; Patou, M.-L.; Debruyne, R.; Couloux, A.; Fernandez, D.A.P.; Wong, S.T.; Fuchs, J.; Jennings, A.P. 2015b. Systematics of the Southeast Asian mongooses (Herpestidae, Carnivora): solving the mystery of the elusive collared mongoose and Palawan mongoose. *Zoological Journal of the Linnean Society* 173: 236-248.
- Veron, G.; Patou, M.-L.; Jennings, A.P. 2015. Molecular systematics of the small-toothed palm civet (*Arctogalidia trivirgata*) reveals a strong divergence of Borneo populations. *Mammalian Biology* 80(40): 347-354.
- Veron, G.; Patou, M.-L.; Tóth, M.; Goonatilake, M.; Jennings, A.P. 2014. How many species of *Paradoxurus* civets are there? New insights from India and Sri Lanka. *Journal Zool Syst and Evol Research* 53(2): 161-174.
- Wilting, A.; Buckley-Beason, V.A.; Feldhaar, H.; Gadau, J.; O'Brien, S.J. Linsenmair, K.E. 2007. Clouded leopard phylogeny revisited: support for species recognition and population division between Borneo and Sumatra. *Frontiers in Zoology* 4:15.
- Wozencraft, W.C. 2005. Order Carnivora. In: *Mammal Species of the World*, Third Edition. Wilson, D.E.; Reeder, D.M. (eds). The Johns Hopkins University Press, Baltimore: 532-628.

Appendix 4 - Repeatability of Linear measurements

In order to estimate the reliability of the data used, we calculated the repeatability of the 35 linear measurements for all species with a number of replicated measurements ≥ 5 specimens (**Tables A4-1 and A4-2**). Repeatability was estimated as the proportion of total variance explained by differences between replicates (i.e. distinct digitisations of the same individual), according to a linear model (Lessels & Boag, 1987). Repeatability was also calculated for supra-specific taxa (genera or groups of related species) for which covariance matrices were estimated (**Table A.4-3**). Repeatability calculated separately for each species and character had average values over 0.93 in all cases; low values were found for BA-OPI in *Arctogalidia trivirgata* (0.52) and for APET-TS in *Crossarchus obscurus* (0.77). Repeatability was much higher when analysing pooled supra-specific data for *Crossarchus* and *Arctogalidia* (minimum repeatability ~ 0.89 for both), suggesting that the lower values might arise from the relatively small number of replicates used for calculating repeatabilities in *A. trivirgata* (10) and *C. obscurus* (15) might be a result of their relatively low numbers of species with replicated measurements. As the minimum repeatability for *Poiana richardsonii* (n=7) and *Prionodon pardicolor* (n=8) is over 0.8, however, other factors may contribute to the low repeatability in *A. trivirgata* and *C. obscurus*.

One further such factor may be that both BA-OPI and APET-TS are measurements composed by landmarks often difficult to identify. BA-OPI is constituted by two type II landmarks, or points of maximum curvature. Also, parts of the foramen magnum were damaged in some specimens, which may have affected these landmarks' digitisation in some specimens. Similarly, the anterior part of the petrosal crest has a gradual lowering in some cases, so that recognition of its anteriormost point (APET) may be somewhat subjective. TS, in turn, is often partially or completely covered by an anterior process extending from the entotympanic bone of the auditory bulla, in which cases this landmark had to be registered to one side of this process, possibly reducing the precision between replicates. Despite these problems, both BA-OPI and APET-TS had high mean and median values (>0.93 in APET-TS and > 0.95 in BA-OPI), so that we considered the use of these measurements would not pose serious limitations to interpretation of the analyses.

Table A4-1: Summary of repeatability values for each linear measurement. The two lowest values are indicated in *underlined italic*

	min	mean	median	max
IS-PM	0.8331	0.9532	0.9664	0.9664
IS-NLE	0.9367	0.9850	0.9902	0.9902
IS-PNS	0.9719	0.9963	0.9977	0.9977
PM-ZS	0.9319	0.9879	0.9921	0.9921
PM-ZI	0.9335	0.9870	0.9925	0.9925
PM-MT	0.9431	0.9887	0.9924	0.9924
NLE-NON	0.9629	0.9927	0.9950	0.9950
NLE-ZS	0.9551	0.9920	0.9954	0.9954
NLE-ZI	0.9614	0.9938	0.9963	0.9963
NON-BR	0.9709	0.9962	0.9975	0.9975
NON-PNS	0.9672	0.9961	0.9973	0.9973
BR-PT	0.9102	0.9877	0.9932	0.9932
BR-APET	0.9229	0.9902	0.9938	0.9938
PT-APET	0.9041	0.9798	0.9858	0.9858
PT-BA	0.9676	0.9931	0.9954	0.9954
PT-EAM	0.8630	0.9808	0.9875	0.9875
PT-ZYGI	0.9519	0.9924	0.9950	0.9950
PT-TSP	0.8312	0.9718	0.9844	0.9844

	min	mean	median	max
ZS-ZI	0.8301	0.9806	0.9887	0.9887
ZI-MT	0.8616	0.9613	0.9698	0.9698
ZI-ZYGI	0.9240	0.9872	0.9912	0.9912
ZI-TSP	0.9589	0.9928	0.9950	0.9950
MT-PNS	0.8865	0.9722	0.9820	0.9820
PNS-APET	0.9544	0.9885	0.9913	0.9913
APET-BA	0.9370	0.9859	0.9889	0.9889
APET-TS	<i><u>0.7719</u></i>	0.9396	0.9482	0.9482
BA-EAM	0.9300	0.9800	0.9874	0.9874
EAM-ZYGI	0.9383	0.9798	0.9853	0.9853
ZYGI-TSP	0.9686	0.9922	0.9948	0.9948
LD-AS	0.9166	0.9844	0.9920	0.9920
BR-LD	0.9240	0.9907	0.9935	0.9935
OPI-LD	0.8453	0.9796	0.9854	0.9854
PT-AS	0.9411	0.9869	0.9916	0.9916
JP-AS	0.8754	0.9664	0.9749	0.9749
BA-OPI	<i><u>0.5223</u></i>	0.9506	0.9723	0.9723

Table A.4-2 - Summary of repeatability values for each species with 5 or more specimens with replicated measurements. The two lowest values are indicated in underlined italic. nreps = number of specimens with replicated measurements.

Family	Species	nreps	min	Mean	median	Max
Eupleridae	<i>Cryptoprocta ferox</i>	34	0.9733	0.9926	0.9950	0.9950
	<i>Eupleres goudotii</i>	18	0.8967	0.9741	0.9783	0.9783
	<i>Fossa fossana</i>	25	0.9143	0.9819	0.9884	0.9884
	<i>Galidia elegans</i>	37	0.8865	0.9684	0.9782	0.9782
	<i>Galidictis fasciata</i>	11	0.8735	0.9662	0.9774	0.9774
	<i>Salanoia concolor</i>	17	0.9042	0.9779	0.9844	0.9844
Felidae	<i>Acinonyx jubatus</i>	30	0.8980	0.9816	0.9906	0.9906
	<i>Caracal caracal</i>	30	0.9396	0.9848	0.9911	0.9911
	<i>Catopuma temminckii</i>	31	0.9650	0.9912	0.9950	0.9950
	<i>Felis catus total</i>	27	0.8606	0.9765	0.9876	0.9876
	<i>Felis margarita</i>	30	0.8312	0.9512	0.9713	0.9713
	<i>Felis silvestris wild</i>	36	0.9086	0.9789	0.9875	0.9875
	<i>Leopardus colocolo</i>	11	0.9822	0.9962	0.9978	0.9978
	<i>Leopardus geoffroyi</i>	32	0.9475	0.9888	0.9930	0.9930
	<i>Leopardus guttulus</i>	41	0.9685	0.9927	0.9952	0.9952
	<i>Leopardus mitis</i>	72	0.9898	0.9978	0.9986	0.9986
	<i>Leopardus tigrinus</i>	8	0.9574	0.9919	0.9941	0.9941
	<i>Leopardus wiedii</i>	45	0.9783	0.9941	0.9951	0.9951
	<i>Leptailurus serval</i>	31	0.8528	0.9726	0.9840	0.9840
	<i>Lynx lynx</i>	22	0.8616	0.9757	0.9849	0.9849
	<i>Lynx rufus</i>	30	0.9465	0.9907	0.9949	0.9949
	<i>Neofelis diardi</i>	25	0.9581	0.9903	0.9941	0.9941
	<i>Neofelis nebulosa</i>	14	0.9416	0.9891	0.9946	0.9946
	<i>Panthera leo</i>	28	0.9041	0.9768	0.9871	0.9871
	<i>Panthera onca</i>	54	0.9942	0.9992	0.9995	0.9995
	<i>Panthera pardus</i>	17	0.9106	0.9794	0.9901	0.9901
	<i>Panthera tigris</i>	15	0.9204	0.9905	0.9952	0.9952
	<i>Panthera uncia</i>	29	0.9323	0.9876	0.9935	0.9935
	<i>Prionailurus bengalensis</i>	30	0.8698	0.9721	0.9799	0.9799
	<i>Puma concolor</i>	43	0.9943	0.9990	0.9993	0.9993
	<i>Puma yagouaroundi</i>	38	0.9742	0.9953	0.9971	0.9971
Herpestidae	<i>Atilax paludinosus</i>	50	0.9378	0.9865	0.9886	0.9886
	<i>Crossarchus obscurus</i>	15	<u>0.7719</u>	0.9506	0.9590	0.9590
	<i>Crossarchus platycephalus</i>	37	0.8995	0.9702	0.9779	0.9779
	<i>Cynictis penicillata</i>	30	0.9230	0.9792	0.9850	0.9850
	<i>Galerella sanguinea central</i>	20	0.8331	0.9658	0.9764	0.9764
	<i>Galerella sanguinea south</i>	14	0.8492	0.9760	0.9828	0.9828
	<i>Helogale parvula</i>	43	0.8715	0.9561	0.9563	0.9563
	<i>Urva javanica</i>	33	0.9061	0.9824	0.9900	0.9900
	<i>Urva urva</i>	32	0.9629	0.9884	0.9914	0.9914
	<i>Mungos mungo</i>	45	0.9137	0.9857	0.9897	0.9897
	<i>Suricata suricatta</i>	41	0.9073	0.9838	0.9880	0.9880
Hyaenidae	<i>Crocuta crocuta</i>	23	0.9793	0.9948	0.9973	0.9973
	<i>Hyaena hyaena</i>	51	0.9737	0.9939	0.9958	0.9958
	<i>Parahyaena brunnea</i>	49	0.9696	0.9935	0.9962	0.9962
	<i>Proteles cristata</i>	31	0.9502	0.9905	0.9944	0.9944
Nandiniidae	<i>Nandinia binotata</i>	49	0.9361	0.9870	0.9912	0.9912
Prionodontidae	<i>Prionodon linsang</i>	13	0.8541	0.9806	0.9889	0.9889
	<i>Prionodon pardicolor</i>	7	0.8453	0.9682	0.9863	0.9863
Viverridae	<i>Arctictis binturong</i>	31	0.9720	0.9949	0.9974	0.9974
	<i>Arctogalidia stigmatica</i>	27	0.9165	0.9872	0.9934	0.9934
	<i>Arctogalidia trivirgata</i>	10	<u>0.5223</u>	0.9722	0.9885	0.9885
	<i>Civettictis civetta</i>	51	0.9508	0.9921	0.9958	0.9958
	<i>Genetta genetta</i>	57	0.8907	0.9723	0.9799	0.9799
	<i>Genetta maculata</i>	59	0.8989	0.9776	0.9840	0.9840
	<i>Genetta servalina</i>	33	0.9049	0.9803	0.9906	0.9906
	<i>Hemigalus derbyanus</i>	30	0.9309	0.9786	0.9858	0.9858
	<i>Paguma larvata</i>	46	0.9546	0.9931	0.9959	0.9959
	<i>Paradoxurus musanga</i>	50	0.9318	0.9896	0.9951	0.9951
	<i>Poiana richardsonii</i>	8	0.8666	0.9720	0.9849	0.9849
	<i>Viverra zibetha</i>	39	0.9379	0.9884	0.9922	0.9922
	<i>Viverricula indica</i>	56	0.8095	0.9710	0.9824	0.9824

Table A.4-3 - Summary of repeatability values for supra-specific taxa for which covariance matrices were estimated. nreps = number of specimens with replicated measurements

Family	Clade	nreps	min	mean	median	max
Eupleridae	<i>Cryptoprocta (Genus)</i>	36	0.9739	0.9934	0.9963	0.9963
Felidae	<i>Leopardus tigrinus group</i>	51	0.9711	0.9942	0.9967	0.9967
	<i>Neofelis (Genus)</i>	39	0.9720	0.9926	0.9958	0.9958
Herpestidae	<i>Crossarchus (Genus)</i>	56	0.8863	0.9744	0.9805	0.9805
	<i>Galerella sanguinea group</i>	35	0.8897	0.9783	0.9819	0.9819
Prionodontidae	<i>Prionodon (Genus)</i>	20	0.8976	0.9813	0.9898	0.9898
Viverridae	Arctogalidia (Genus)	37	0.8972	0.9865	0.9934	0.9934

References

Lessels, C.M.; Boag, P.T. 1987. Unrepeatable repeatabilities: A common mistake. The Auk 104: 116-121.

Appendix 5 - Extended Methods: Identification of external sources of variation and estimation of phenotypic covariance matrices

The process for estimating phenotypic covariance matrices involved two steps: identification and correction of external sources of variation not relevant for the present study (e.g. sex, geographic variation/subspecies, age, captivity effects) based on linear models, and matrix estimation using the residuals of the appropriate linear model.

Identification of significant external sources of variation considered four factors: age, captivity, sex and subspecies (or species and subspecies for supra-specific taxa). As explained below, *Felis catus* involved historical time as a factor instead of subspecies. The procedures used to classify specimens within each factor are detailed below.

Only two "age" categories were recognised (adult and young adult), since only specimens with practically completely erupted dentition were digitised. Classification of specimens in this factor was done during data collection, based on the state of the teeth and suture closure (particularly for the basioccipital-basisphenoid suture).

The "captivity" factor was used to assess possible differences between wild specimens and animals which lived part of, or all their lives in captivity. Specimens were classified for this factor based mainly on information available in museum tags, databases and/or registry books. Specimens without information of captivity status and without clear skull alterations indicative of life in captivity were classified as wild.

For the factors "sex" and "subspecies", classification was done in two stages. For "sex", the initial classification used information present in museum tags or databases. Specimens without information in this respect and/or with conflicting information in different sources were considered to be of "unknown sex".

For "subspecies", an extensive literature review on infra-specific taxonomy and systematics was carried out to determine the geographic subspecies (considered here to include effects of geographic variation) to be considered for each Feliformian species and the geographic range of each one. After this step, initial definition of subspecies was performed based on detailed assessment of information on collection localities for each specimen in an attempt to determine their exact or approximate location, followed by classification of each individual with sufficient information within a particular subspecies. As collection localities are often too general (e.g. "Madagascar"), inaccurate

(e.g. listing ports from which the material was shipped instead of the actual collection locality) or may present errors or particularities in spelling due to the language used by collectors. Locations described may also be incorrect in some cases, reflecting the knowledge of the person responsible for the specimen at the time of its deposit. For these reasons, interpretation of locality data is not always a simple, straightforward process. When a location could not be defined, or when the location given was likely wrong, specimens were initially considered of "unknown subspecies". In other cases, the information available was not precise enough to determine a single most likely subspecies, but could define that a specimen belonged to one among a subgroup of the subspecies considered for its species. The literature review and these particularities were rather time-intensive processes, but they allowed the analysis of subspecies differences for all non-monotypic species with relevant variation in the locations of digitised specimens, allowing more reliable estimate of within-population variation. A list of the subspecies considered for initial classification within each species for this work is provided in **Appendix 20**.

For the domestic cat (*Felis catus*), geographic variation was not considered a relevant information, and no information was available regarding the breeds of the specimens sampled. However, the dataset used for *F. catus* included both recent specimens and mummified domestic cat skulls (located within the felid collection of the *Museum für Naturkunde* in Berlin - ZMB_Mam -, previously unknown to the museum's team), allegedly from the 12nd Egyptian cats according to documents found along with the skulls. Considering this origin information is correct, there might be differences in skull form between recent and mummified specimens. The factor "historical time" (distinguishing recent specimens and mummified skulls) was therefore included in the analysis of external sources of variation for this species. It should be noted that future studies to confirm the authenticity of these skulls and compare them to recent specimens might be an interesting topic for future studies.

During the next stage after the initial classification of "sex" and "subspecies", Principal Coordinate Analysis of the set of 35 linear measurements were performed for all species including specimens with "unknown" sex or subspecies classifications, in order to assess the distribution of sexes and subspecies in character space. This procedure was followed by linear discriminant analyses (LDA) on the principal components or a subset thereof to perform the classification of specimens previously

unclassified for sex and subspecies.

Whenever there were individuals with unknown classification for both factors (sex and subspecies) and the sample size of classified individuals was sufficient for univariate ANOVAs, we tested for the existence of interaction between factors before reclassification. Interaction effects were not recognised at this point for any species. Therefore, specimens were classified for each factor independently in all cases, starting with the factor with more distinctive differences between groups (according to visual analysis of the PCA, or to the number of preliminary univariate ANOVAs recognising significant differences). Although the results of cross-validation tests on the 'training set' used for reclassification of sex and subspecies was sometimes relatively low (which might produce spurious classifications), these cases corresponded to those in which differences between factors (sexes or subspecies) were small. Spurious classifications in these cases were likely not a problem for further analyses, since a small difference between factors is unlikely to be considered significant in the tests for identification of significant external factors of variation (see below). The alternative of using only specimens which could be classified based on the original sex and locality information would lead to a significant reduction in available sample sizes, and therefore the use of reclassifications using LDA was considered a more appropriate option.

After reclassification of the "sex" and "subspecies" factors, the identification of significant external sources of variations was done for all species/taxa using MANOVAs (whenever possible for the available sample size) and univariate ANOVAs. The selection of external sources of variation to be corrected was based on significance in MANOVA tests, and/or a high number of characters significant on univariate ANOVAs, as well as on effect sizes. The effects included in the final linear model chosen for each species may be seen in **Table 2-1 (Chapter 2)**.

After choosing the most appropriate linear model for each species, covariance matrix estimation was carried out using the residuals of the selected model and the R function "CalculateMatrix" ("evolqg" package; Melo *et al*, 2015). Correlation matrices were then generated from the covariance matrices using the "cov2cor" function.

Better-estimated covariance matrices were also estimated for some supra-specific taxa including species with lower sample sizes: *Cryptoprocta* (*C. ferox* plus the subfossil *C. spelaea*, previously considered as a synonym of the current species - Savage, 1978; Köhncke & Leonhardt, 1986; but see Goodman *et al*, 2004); *Leopardus*

tigrinus group (*Leopardus tigrinus* and *Leopardus guttulus*); *Neofelis* (*N. nebulosa* and *N. diardi*); *Crossarchus* (*C. obscurus*, *C. platycephalus* and *C. alexandri*); *Galerella sanguinea* group (*Galerella sanguinea* central *Galerella sanguinea* south and *Galerella ochracea*; no data could be collected for *G. flavescens* and *G. nigrata*); *Prionodon* (*Prionodon linsang* and *P. pardicolor*) and *Arctogalidia* (*A. trivirgata* e *A. stigmatica*). The method used to identify significant external sources of variation for these taxa was as described above, but the factor "subspecies" exchanged by "species/subspecies", having as categories a set including the species in the group and the subspecies considered significant in species-level analyses for each species. Matrix estimation then proceeded as described above. Sample sizes and the linear models chosen for supra-specific matrices are also shown in **Table 2-1 (Chapter 2)**.

References

- Goodman, S.M.; Rasoloarison, R.M.; Ganzhorn, J.U. 2004. On the specific identification of subfossil *Cryptoprocta* (Mammalia, Carnivora) from Madagascar. *Zoosystema* 26(1): 129-143.
- Köhncke, M.; Leonhardt, K. 1986. *Cryptoprocta ferox*. *Mammalian Species* 254:1-4.
- Melo, D.; Garcia, G.; Hubbe, A. Assis, A.P.; Marroig, G. 2015. *evolqg* - An R package for evolutionary quantitative genetics [version 1; referees:1 approved, 1 approved with reservations] F1000 Research 4:925.
- Savage, R.J.G. 1978. Carnivora. In: Maglio, V.J. & Cooke, H.B.S. (eds) *Evolution of African Mammals*. Harvard University Press, Cambridge, Massachusetts: 97-122.

Appendix 6 - Rarefaction analyses for taxa from different families

Fig A6-1 - Rarefaction analysis on the *Civettictis civetta* **P** matrix and distribution of pairwise similarities within different taxonomic levels (between families, within families and within a genus), using the Random Skewers (RS) method. The horizontal line indicates the median value of pairwise similarities within families. Vertical lines indicate the distribution of similarities for $n=35$ (number of characters), $n=17$ and $n=7$ (minimum sample sizes here for better-estimated matrices and for species-level matrices).

Fig A6-2 - Rarefaction analysis on the *Hyaena hyaena* **P** matrix and distribution of pairwise similarities within different taxonomic levels (between families, within families and within a genus), using the Random Skewers (RS) method. The horizontal line indicates the median value of pairwise similarities within families. Vertical lines indicate the distribution of similarities for $n=35$ (number of characters), $n=17$ and $n=7$ (minimum sample sizes here for better-estimated matrices and for species-level matrices).

Fig A6-3 - Rarefaction analysis on the *Crossarchus* (Genus) **P** matrix and distribution of pairwise similarities within different taxonomic levels (between families, within families and within a genus), using the Random Skewers (RS) method. The horizontal line indicates the median value of pairwise similarities within families. Vertical lines indicate the distribution of similarities for $n=35$ (number of characters), $n=17$ and $n=7$ (minimum sample sizes here for better-estimated matrices and for species-level matrices).

Appendix 7 - Results for Random Skewers (RS) matrix similarities adjusted using a regression of similarity on the inverse of the harmonic mean based on rarefaction (Steppan, 1997)

Fig A7-1 - Heatmap (A) and PCO (B) for 63 species-level matrices using similarities adjusted using a regression of similarity on the inverse of the harmonic mean, based on the rarefaction analysis of a pooled *Felis catus* + *silvestris* matrix. Results based on a rarefaction of the *Leopardus mitis* matrix are very similar and therefore not shown.

Fig A7-2 - Heatmap (A) and PCO (B) for the 53 better-sampled taxa using similarities adjusted using a regression of similarity on the inverse of the harmonic mean, based on the rarefaction analysis of a pooled *Felis catus* + *silvestris* matrix. Results based on a rarefaction of the *Leopardus mitis* matrix are very similar and therefore not shown.

References

Steppan, S.J. 1997. Phylogenetic analysis of phenotypic covariance structure. I. Contrasting results from Matrix Correlation and Common Principal Component Analyses. *Evolution* 51(2) 571-586.

Appendix 8 - Morphospace and Ecospace for diet and sociality

Figure A8-1 - Proportion of variation represented by each axis of a Principal Coordinate Analysis (%Variation) compared to the proportion of variation explained by eigenvalues of random data (Broken Stick Model - Frontier, 1976) for Matrix Similarity (63 and 53 taxa), Mean Morphology, Diet and Sociality. The number of PCO axes which explain more variation than expected by chance is: 7 for Matrix Similarity - 63 species, 5 for Matrix Similarity - 53 taxa; 3 for Mean Morphology; 4 for Diet and 2 for Sociality.

Figure A8-2 - Integration space formed by the third and fourth axes of a Principal Coordinate Analysis (PCO) run on Matrix Similarity results for the 63 species-level matrixes. The third and fourth PCO axes jointly explain 18.46% of total variation in integration patterns.

Figure A8-3 - Integration space formed by the third and fourth axes of a Principal Coordinate Analysis (PCO) run on Matrix Similarity results for the 53 taxa with better-estimated matrixes. The third and fourth PCO axes jointly explain 17.52% of total variation in integration patterns.

Figure A8-4 - Morphospace formed by the two first axes of a Principal Coordinate Analysis (PCO) run on the Mahalanobis distance matrix for the 53 taxa with better-estimated matrices. The two first PCO axes explain 72.78% of total variation in average morphology.

Figure A8-5 - Morphospace formed by the second and third axes of a Principal Coordinate Analysis (PCO) run on the Mahalanobis distance matrix for the 53 taxa with better-estimated matrices. The second and third PCO axes jointly explain 28.73% of total variation in average morphology.

Figure A.8-6 - Diet ecospace formed by the two first axes of a Principal Coordinate Analysis (PCO) run on the diet dissimilarity matrix (DDM) for the 53 taxa with better-estimated matrices. Arrows indicate the correlation of PCOs axes with each dietary item and with 'diet breadth' (i.e. sum of the score for all dietary items). The two first PCO axes explain 63.54% of the total variation in diets.

Figure A.8-7 - Diet ecospace formed by the third and fourth axes of a Principal Coordinate Analysis (PCO) run on the diet dissimilarity matrix (DDM) for the 53 taxa with better-estimated matrices. Arrows indicate the correlation of PCOs axes with each dietary item and with 'diet breadth' (i.e. sum of the score for all dietary items). The third and fourth PCO axes jointly explain 25.03% of the total variation in diets.

Figure A.8-8 - Social behaviour ecospace formed by the two first axes of a Principal Coordinate Analysis (PCO) run on the sociality dissimilarity matrix (SDM) for the 50 taxa with better-estimated matrices and available information on sociality. Arrows indicate the correlation of PCOs axes with each type of social behaviour. The two first PCO axes explain 93.24% of the total variation in social behaviour.

Figure A.8-9 - Plot of integration magnitude indexes (r^2 - x axis) versus the first axis of a Principal Coordinate Analysis (PCO) run on Matrix Similarity results for the 53 better-estimated matrices (y axis - explains 27.50% of the total variance in integration patterns).

References

Frontier, S. 1976. Étude de la décroissance des valeurs propres dans une analyse en composantes principales: comparaison avec le modèle de baton brisé. *Journal of Experimental Marine Biology and Ecology* 25: 67-75.

Appendix 9 - Matrix comparisons using the Krzanowski Correlation (Krz) method (Krzanowski, 1979)

Figure A9-1. Pairwise comparisons (Krz) between the 63 species-level matrices (A) and position of each species in the Integration Space defined by the 2 first PCOs (B).

Figure A9-2. Pairwise comparisons (Krz) between the 53 better-estimated matrixes (A) and position of taxa in the Integration Space defined by the 2 first PCOs (B).

References

Krzanowski, W.J. 1979. Between-Groups Comparison of Principal Components. *Journal of the American Statistical Association* 74(367): 703.

Appendix 10 - Analysis of sex-specific *P* matrixes

Figure A10-1. Random Skewers (RS) similarity between sex-specific and 'complete' matrixes (including specimens from both sexes) for each species. The red line indicates average similarity (0.901). Colours represent the sample size used to build each sex-specific matrix, with lower samples closer to dark red and larger samples closer to dark blue. Notice that lower similarities are found mainly for low or very low sample sizes.

Figure A10-2. Regression of Random Skewers similarity values on the inverse of the harmonic mean between the sample size of complete matrixes and sex-specific matrixes, showing the influence of sample size on similarity values. $R^2 = 0.64$, $p < 0.001$.

Figure A10-3. Random Skewers (RS) similarity between male and female matrices for each species. The red line indicates average similarity (0.778). Colours represent the sample size used to build each sex-specific matrix, with lower samples closer to dark red and larger samples closer to dark blue. The largest sample sizes are close to 30 specimens.

Figure A10-4. Regression of Random Skewers similarity values on the harmonic mean between the sample sizes of male and female matrices for each species, showing the influence of sample size on similarity values. $R^2 = 0.62$, $p < 0.001$.

Figure A10-5. Comparison of bootstrapped distribution of integration magnitudes (r^2) between male and female matrices for each species. Males and females for each species are presented side-by-side. The colour filling the boxplots represents the sample size for each sex-specific matrix, with lower samples closer to dark red and larger samples closer to dark blue. Notice that larger r^2 differences between sexes are mainly found when one sex has low or very low sample sizes.

Figure A10-6. Regression of the square root of calculated r^2 values on the sample sizes of male and female matrices for each species. The influence of sample size is non-significant. $R^2 = 0.02$, $p=0.138$.

Figure A10-7. Regression of the standard deviation of bootstrapped r^2 values on sample size for male and female matrices for each species, showing significantly increased variance on r^2 estimates with lower sample sizes. $R^2 = 0.13$, $p < 0.001$.

Appendix 11 - Assessment of relationship between estimated integration magnitude (r^2) and sample size

Figure A11-1. Regression of the square root of estimated integration magnitude (r^2) on sample size for the 53 better-estimated matrices. The influence of sample size on estimated is non-significant. $R^2 = 0.007$, $p=0.549$.

Figure A11-2. Regression of the standard deviation of bootstrapped r^2 values on sample size for the 53 better-estimated matrices. The variance of r^2 estimates seems to increase with lower sample sizes; the regression is significant for $\alpha = 0.10$. $R^2 = 0.055$, $p = 0.0923$.

Figure A11-3. Regression of the standard deviation of bootstrapped r^2 values on sample size for the 51 matrices with $n \geq 20$ (removing *Eupleres goudotii* and *Salanoia concolor* from the set of 53 matrices). The relationship between r^2 estimates and sample sizes is no longer significant for $n \geq 20$. $R^2 = 0.037$, $p = 0.176$.

Appendix 12 - Phylogeny used and generation of Phylogenetic Distance Matrix

As described in the section of the Introduction (Chapter 1) which deals with the group studied in this dissertation (Feliformia), we decided to use for this work the supertree from Nyakatura & Bininda-Emonds (2012) with best estimate of divergence times as a basis, changing it to reflect some results of recent studies. Initially, these alterations were done so as to produce a tree including all recognised Feliformia species. However, since the phylogeny was used here only for analyses related to morphological integration, we describe here only changes including species/taxa which could be used in these analyses (i.e. taxa for which phenotypic covariance were estimated - see **Table 2-1**). Changes in the phylogeny and the calculation of phylogenetic distances were performed using the R package "ape" (Paradis *et al*, 2004), and are described below.

First of all, species included in Nyakatura & Bininda-Emonds (2012)'s tree considered here as synonyms of other species were dropped from the tree, using the function "drop.tip" (package "ape"). This procedure was used to remove *Prionailurus iriomotensis* (considered here a subspecies of *Pr. bengalensis*), *Leopardus braccatus* and *L. pajeros* (both considered here as subspecies of *L. colocolo*).

After that, species not present in Nyakatura & Bininda-Emonds (2012)'s supertree were included. Most of these are recently described species previously considered part of species already included in the phylogeny. The divergence times for the splits between species for those cases had to be considered on a case-by-case basis, as described below.

Leopardus mitis was initially added as a sister species to *L. pardalis*, following Nascimento (2010)'s suggestion, which is at least partially supported by Janečka *et al* (2007) and Ruiz-Garcia *et al* (2012)'s results. As the sample obtained for *L. pardalis* (from Central and North America) was not enough for **P** matrix estimation, only *L. mitis* was kept in the final tree. Therefore, a divergence time did not have to be estimated in this case.

Leopardus guttulus was added as the sister species to *L. tigrinus*, following Trigo *et al* (2013). The divergence time used for this split corresponded to the one provided in the supplementary material of the article describing *L. guttulus* (0.53 mya).

Neofelis diardi was added as sister to *N. nebulosa*, with a divergence time based on the results of Li *et al* (2016): ~1.65 mya.

Arctogalidia stigmatica was added as the sister group to *A. trivirgata*, following Veron *et al* (2015a). The article does not provide a possible divergence time for the split between these species, but argues that the large genetic difference between specimens from Borneo (*A. stigmatica*) and Southeast Asia (*A. trivirgata*) is similar to that seen in other mammals, and corresponds to a time when connections between Borneo and the other Sunda islands were limited. Two possible times with higher sea levels, corresponding to this description, were considered: ~3.9 mya (as during a split between *Paradoxurus* species according to Patou *et al*, 2010) and ~1.65 (as during the split between *Neofelis* species). For this work, we chose to use the most recent divergence date (1.65mya).

For *Paradoxurus musanga*, *P. phillipinensis* and *P. hermaphroditus*, we initially used the topology proposed by Veron *et al* (2014), with *musanga* as the sister species to *phillipinensis*. As a sample size sufficient for **P** matrix estimation was obtained only for *P. musanga*, this was the only species kept in the final tree used here, and therefore divergence times between species in this genus were also not relevant for our purposes.

For *Galerella*, we initially used Rapson *et al* (2012)'s cytochrome b tree topology as a basis, considering *Galerella sanguinea* to be divided into two possible species: "*Galerella sanguinea south*", from South Africa, as a sister group to *Galerella nigrata*, and "*Galerella sanguinea central*", from Central and East Africa as a sister to (*G. sanguinea south* + *G. nigrata*). As Rapson *et al* (2012) did not provide divergence dates, and **P** matrix estimation was possible only for *Galerella sanguinea south* and *Galerella sanguinea central*, in this case a rough estimate of the likely divergence time between these species/lineages was performed based on the number of substitutions provided in Rapson *et al* (2012) and the date of 8 mya for the split between *Galerella* and *Herpestes ichneumon* provided in Nyakatura & Bininda-Emonds (2012)'s tree. This produced an estimated divergence time of ~5 mya between *Galerella sanguinea south* and *Galerella sanguinea central*.

Except for the change in the name of the genus, no changes were done to *Urva* species (Asiatic mongooses, previously included in *Herpestes*), in spite of our decision to follow Patou *et al* (2009) and Veron *et al* (2015b)'s topology, since **P** matrices could be estimated only for *Urva javanica* and *Urva urva*. Given the large difference in divergence times for Herpestidae between Patou *et al* (2009) and Nyakatura & Bininda-Emonds (2012), we decided not to alter divergence times within this family for this

work. The large disparity between the divergence times in Herpestidae is likely due to the use of more precise calibration points by Patou *et al* (2009) (*Leptoplesictis*, 18 mya, as a minimum time limit for Herpestidae, and 7 mya as a minimum time limit for *Galerella* - Peigné *et al*, 2005), so it is in fact likely that Patou *et al* (2009)'s dates may be more accurate. That notwithstanding, the effects of this disparity spread throughout the family, which would necessitate a number of changes in divergence times for many species in the base tree. It was therefore decided to keep Nyakatura & Bininda-Emonds (2012)'s dating for Herpestidae, in order to limit the number of necessary changes.

As described in Chapter 2, analyses using the phylogeny were actually limited to the 53 better-estimated matrices. Therefore, the decisions taken regarding divergence times between *Leopardus guttulus* - *L. tigrinus*, *Galerella sanguinea central* and *G.s.south*, *Neofelis diardi* - *N. nebulosa* and *Arctogalidia* species did not affect our results, since these clades were represented as single groups in the phylogeny effectively used for the analyses (*Leopardus tigrinus* group; *Galerella sanguinea* group; *Neofelis* genus and *Arctogalidia* genus).

The changes done to the tree used here reflect part of the more recent knowledge on phylogenetic relationships within Feliformia. Some of the most recent results (e.g. *Arctogalidia* positioned within a monophyletic Paradoxurinae subfamily separate from Hemigalinae - Wilting & Fickel, 2012; Patou *et al*, 2008) were ignored here, however, because larger inconsistencies between these results and the base tree used would require greater changes and further rough calculations of divergence dates. The persistence of some inconsistencies between the most recent phylogenetic hypotheses focused on different parts of Feliformia bring attention to the necessity of an updated species-level phylogeny for the suborder, and in fact for Carnivora as a whole, including recent results and newly published sequences; generating such an updated phylogeny, however, would be outside the scope of the present work. Despite these limitations, the phylogeny used is hopefully a reasonable approximation of the current knowledge of phylogenetic relations within Feliformia, and is expected to provide a consistent basis for representative comparisons with integration patterns and magnitudes. The final phylogeny generated is shown in **Figure A12-1**. The 53 species and supra-specific taxa represented in **bold** are those with better-estimated **P** matrices which were in fact used for analyses based on the phylogeny.

Phylogenetic distances were obtained from the final phylogeny using the

function "cophenetic" (package "ape"). We initially obtained phylogenetic distance matrices considering divergence dates as branch lengths, as well as patristic ('node') distances calculated from a tree in which all branch lengths were converted to a length of 1. Mantel Tests between phylogenetic distance matrices produced with both methods ('branch length' and 'node length') indicated significant similarity, but with a relatively low value of 0.732 (for the 53 better-estimated taxa). This possibly reflects the approximation of originally very divergent clades when converting branch lengths to 1 (e.g. Prionodontidae and Felidae). For this reason, all further analyses focused on distances calculated with divergence dates as branch lengths.

Figure A12-1 - Phylogeny used in the present work, including the 63 species for which phenotypic covariance matrices (P) were estimated. Clades (species, genera or groups of species) in **bold** are the 53 with better-estimated matrices ($n \geq 17$) effectively used in analyses comparing integration with the phylogeny. The figure also indicates other relevant taxonomic groups mentioned in Chapters 1, 2 and 3.

References

- Janečka, J.E.; Walker, C.W.; Tewes, M.E.; Caso, A.; Laack, L.L.; Honeycutt, R.L. 2007. Phylogenetic relationships of ocelot (*Leopardus pardalis albens*) populations from the Tamaulipan Biotic Province and Implications for Recovery. *The Southwestern Naturalist* 52(1): 89-96.
- Li, G.; Davis, B.W.; Eizirik, E.; Murphy, W.J. 2016. Phylogenomic evidence for ancient hybridization in the genomes of living cats (Felidae). *Genome Research* 26(1): 1-11. doi: 10.1101/gr.186668.114.
- Nascimento, F.O. 2010. Revisão taxonômica do gênero *Leopardus* Gray, 1842 (Carnivora, Felidae). Doctoral dissertation, Instituto de Biociências, Universidade de São Paulo.
- Nyakatura, K.; Bininda-Emonds, O.R.P. 2012. Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. *BMC Biology* 10(12): doi:10.1186/1741-7007-10-12
- Paradis, E.; Claude, J.; Strimmer, K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20: 289-290.
- Patou, M.-L.; Mclenachan, P.A.; Morley, C.G.; Couloux, A.; Jennings, A.P.; Veron, G. 2009. Molecular phylogeny of the Herpestidae (Mammalia, Carnivora) with a special emphasis on the Asian Herpestes. *Molecular Phylogenetics and Evolution* 53: 69-80.
- Patou, M.-L.; Wilting, A.; Gaubert, P.; Esselstyn, J.A.; Cruaud, C.; Jennings, A.P.; Fickel, J.; Veron, G. 2010. Evolutionary history of the *Paradoxurus* palm civets - a new model for Asian biogeography. *Journal of Biogeography* 37(11): 2077-2097
- Patou, M.-L.; Debruyne, R.; Jennings, A.P.; Zubaid, A.; Rovie-Ryan, J.J.; Veron, G. 2008. Phylogenetic relationships of the Asian palm civets (Hemigalinae & Paradoxurinae, Viverridae, Carnivora). *Molecular Phylogenetics and Evolution* 47: 883-892.
- Peigné, S.; de Bonis, L.; Likius, A.; Ta Mackaye, H.; Vignaud, P.; Brunet, M. 2005. The earliest modern mongoose (Carnivora, Herpestidae) from Africa (late Miocene of Chad). *Naturwissenschaften* 92: 287-292.
- Rapson, S.A.; Goldizen, A.W.; Seddon, J.M. 2012. Species boundaries and possible hybridization between the black mongoose (*Galerella nigrata*) and the slender mongoose (*Galerella sanguinea*). *Molecular Phylogenetics and Evolution* 65: 831-839.
- Ruiz-Garcia, M.; Corrales, C.; Pinedo-Castro, M. 2012. Craniometric and Microsatellite genetic differentiation among putative ocelot subspecies (*Leopardus pardalis*) throughout Latin America. In: *Molecular Population Genetics, Phylogenetics, Evolutionary Biology and Conservation of the Neotropical Carnivores*. Ruiz-Garcia, M.; Shostell, J. (eds). Nova Science Publishers, Inc., New York (USA).
- Trigo, T.C.; Schneider, A.; Oliveira, T.G.; Lehugeur, L.M.; Silveira, L.; Freitas, T.R.O.; Eizirik, E. 2013. Molecular Data Reveal Complex Hybridization and a Cryptic Species of Neotropical Wild Cat. *Current Biology* 23: 1-6.
- Veron, G.; Patou, M.-L.; Debruyne, R.; Couloux, A.; Fernandez, D.A.P.; Wong, S.T.; Fuchs, J.; Jennings, A.P. 2015b. Systematics of the Southeast Asian mongooses (Herpestidae, Carnivora): solving the mystery of the elusive collared mongoose and Palawan mongoose. *Zoological Journal of the Linnean Society* 173: 236-248.
- Veron, G.; Patou, M.-L.; Jennings, A.P. 2015a. Molecular systematics of the small-toothed palm civet (*Arctogalidia trivirgata*) reveals a strong divergence of Borneo populations. *Mammalian Biology* 80(40): 347-354.
- Veron, G.; Patou, M.-L.; Tóth, M.; Goonatilake, M.; Jennings, A.P. 2014. How many species of *Paradoxurus* civets are there? New insights from India and Sri Lanka. *Journal Zool Syst and Evol Research* 53(2): 161-174.
- Wilting, A.; Fickel, J. 2012. Phylogenetic relationship of two threatened endemic viverrids from the Sunda Islands, Hose's civet and Sulawesi civet. *Journal of Zoology* 288(3): 184-190

Appendix 13 - Feliformia dietary and social behaviour databases.

Table A13-1 - Dietary information database for Feliformia. 3 = consumed preferentially; 2 = often consumed; 1 = sometimes consumed; 0 = not consumed / no information.

Family	Genus	Species	Animal	Vertebrate	Mammal	Bird	Herptile	Fish	Invertebrate	Plant	Seed	Fruit	Root	Leaf	Other Plant
EUPLERIDAE	<i>Cryptoprocta</i>	<i>ferox</i>	3	3	3	3	2	0	2	0	0	0	0	0	0
	<i>Cryptoprocta</i>	<i>spelaea</i>	3	3	3	3	2	0	2	0	0	0	0	0	0
	<i>Eupleres</i>	<i>goudotii</i>	3	2	0	0	2	0	3	0	0	0	0	0	0
	<i>Fossa</i>	<i>fossana</i>	3	3	0	0	3	3	3	0	0	0	0	0	0
	<i>Galidia</i>	<i>elegans</i>	3	3	3	3	3	2	2	2	0	2	0	0	0
	<i>Galidictis</i>	<i>fasciata</i>	3	3	3	0	0	0	2	0	0	0	0	0	0
	<i>Galidictis</i>	<i>grandidieri</i>	3	3	3	0	0	0	2	0	0	0	0	0	0
	<i>Mungotictis</i>	<i>decemlineata</i>	3	2	0	0	0	0	3	0	0	0	0	0	0
	<i>Salanoia</i>	<i>concolor</i>	3	2	2	0	2	0	3	3	0	3	0	0	0
FELIDAE	<i>Acinonyx</i>	<i>jubatus</i>	3	3	3	0	0	0	0	0	0	0	0	0	0
	<i>Caracal</i>	<i>aurata</i>	3	3	3	3	0	0	0	0	0	0	0	0	0
	<i>Caracal</i>	<i>caracal</i>	3	3	3	3	0	0	0	0	0	0	0	0	0
	<i>Felis</i>	<i>chaus</i>	3	3	3	3	3	0	0	0	0	0	0	0	0
	<i>Felis</i>	<i>margarita</i>	3	3	3	2	2	0	0	0	0	0	0	0	0
	<i>Felis</i>	<i>nigripes</i>	3	3	3	3	3	0	0	0	0	0	0	0	0
	<i>Felis</i>	<i>silvestris</i>	3	3	3	2	2	0	2	0	0	0	0	0	0
	<i>Felis</i>	<i>bieti</i>	3	3	3	2	2	0	2	0	0	0	0	0	0
	<i>Felis</i>	<i>catus</i>	3	3	3	2	2	0	2	0	0	0	0	0	0
	<i>Leopardus</i>	<i>colocolo</i>	3	3	3	3	0	0	0	0	0	0	0	0	0
	<i>Leopardus</i>	<i>geoffroyi</i>	3	3	3	2	2	2	0	0	0	0	0	0	0
	<i>Leopardus</i>	<i>guigna</i>	3	3	3	3	0	0	0	0	0	0	0	0	0
	<i>Leopardus</i>	<i>jacobita</i>	3	3	3	0	0	0	0	0	0	0	0	0	0
	<i>Leopardus</i>	<i>pardalis</i>	3	3	3	3	3	3	0	0	0	0	0	0	0
	<i>Leopardus</i>	<i>mitis</i>	3	3	3	3	3	3	0	0	0	0	0	0	0
	<i>Leopardus</i>	<i>tigrinus</i>	3	3	3	3	3	0	0	0	0	0	0	0	0
	<i>Leopardus</i>	<i>guttulus</i>	3	3	3	3	3	0	0	0	0	0	0	0	0
	<i>Leopardus</i>	<i>pardinoides</i>	3	3	3	3	3	0	0	0	0	0	0	0	0
	<i>Leopardus</i>	<i>wiedii</i>	3	3	3	2	0	0	0	2	0	2	0	0	0
	<i>Leptailurus</i>	<i>serval</i>	3	3	3	0	0	0	0	0	0	0	0	0	0
	<i>Lynx</i>	<i>canadensis</i>	3	3	3	2	0	2	0	0	0	0	0	0	0
	<i>Lynx</i>	<i>lynx</i>	3	3	3	2	0	0	0	0	0	0	0	0	0
	<i>Lynx</i>	<i>pardinus</i>	3	3	3	2	0	0	0	0	0	0	0	0	0
	<i>Lynx</i>	<i>rufus</i>	3	3	3	3	0	0	0	0	0	0	0	0	0
	<i>Neofelis</i>	<i>diardi</i>	3	3	3	0	0	0	0	0	0	0	0	0	0
	<i>Neofelis</i>	<i>nebulosa</i>	3	3	3	0	0	0	0	0	0	0	0	0	0
	<i>Otocolobus</i>	<i>manul</i>	3	3	3	2	0	0	0	0	0	0	0	0	0
	<i>Panthera</i>	<i>leo</i>	3	3	3	0	0	0	0	0	0	0	0	0	0
	<i>Panthera</i>	<i>onca</i>	3	3	3	0	2	2	0	0	0	0	0	0	0
	<i>Panthera</i>	<i>pardus</i>	3	3	3	1	0	0	1	0	0	0	0	0	0
	<i>Panthera</i>	<i>tigris</i>	3	3	3	1	0	0	0	0	0	0	0	0	0
	<i>Panthera</i>	<i>uncia</i>	3	3	3	0	0	0	0	0	0	0	0	0	0

Family	Genus	Species	Animal	Vertebrate	Mammal	Bird	Herptile	Fish	Invertebrate	Plant	Seed	Fruit	Root	Leaf	Other Plant
FELIDAE	<i>Catopuma</i>	<i>badia</i>	3	3	3	3	3	0	0	0	0	0	0	0	0
	<i>Catopuma</i>	<i>marmorata</i>	3	3	2	3	1	0	0	0	0	0	0	0	0
	<i>Catopuma</i>	<i>temminckii</i>	3	3	3	3	3	0	0	0	0	0	0	0	0
	<i>Prionailurus</i>	<i>bengalensis</i>	3	3	3	3	3	3	0	0	0	0	0	0	0
	<i>Prionailurus</i>	<i>planiceps</i>	3	3	2	0	0	3	0	0	0	0	0	0	0
	<i>Prionailurus</i>	<i>rubiginosus</i>	3	3	3	0	1	0	0	0	0	0	0	0	0
	<i>Prionailurus</i>	<i>viverrinus</i>	3	3	2	2	2	3	2	0	0	0	0	0	0
	<i>Puma</i>	<i>concolor</i>	3	3	3	0	0	0	0	0	0	0	0	0	0
	<i>Puma</i>	<i>yagouaroundi</i>	3	3	3	3	3	0	0	0	0	0	0	0	0
HERPESTIDAE	<i>Atilax</i>	<i>paludinosus</i>	3	3	3	0	3	3	3	3	0	3	0	0	0
	<i>Bdeogale</i>	<i>crassicauda</i>	3	2	2	0	0	0	3	0	0	0	0	0	0
	<i>Bdeogale</i>	<i>jacksoni</i>	3	3	3	0	0	0	0	0	0	0	0	0	0
	<i>Bdeogale</i>	<i>nigripes</i>	3	2	0	0	0	0	3	0	0	0	0	0	0
	<i>Bdeogale</i>	<i>omnivora</i>	3	0	0	0	0	0	3	0	0	0	0	0	0
	<i>Crossarchus</i>	<i>alexandri</i>	3	3	0	0	3	0	3	3	0	3	0	0	0
	<i>Crossarchus</i>	<i>ansorgei</i>	3	3	0	0	3	0	3	3	0	3	0	0	0
	<i>Crossarchus</i>	<i>obscurus</i>	3	3	0	0	3	0	3	3	0	3	0	0	0
	<i>Crossarchus</i>	<i>platycephalus</i>	3	3	0	0	3	0	3	3	0	3	0	0	0
	<i>Cynictis</i>	<i>penicillata</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Dologale</i>	<i>dybowskii</i>	3	0	0	0	0	0	3	0	0	0	0	0	0
	<i>Helogale</i>	<i>hirtula</i>	3	2	0	0	0	0	3	2	0	2	0	0	0
	<i>Helogale</i>	<i>parvula</i>	3	1	0	0	0	0	3	0	0	0	0	0	0
	<i>Urva</i>	<i>brachyura</i>	3	3	3	3	3	3	3	3	0	3	0	0	3
	<i>Urva</i>	<i>edwardsii</i>	3	3	0	0	3	0	3	0	0	0	0	0	0
	<i>Galerella</i>	<i>flavescens</i>	3	3	3	3	3	3	3	3	0	3	0	0	3
	<i>Urva</i>	<i>fusca</i>	3	3	3	3	3	3	3	3	0	3	0	0	3
	<i>Herpestes</i>	<i>ichneumon</i>	3	3	3	3	3	3	3	2	0	2	0	0	0
	<i>Urva</i>	<i>javanica</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Urva</i>	<i>auropunctata</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Xenogale</i>	<i>naso</i>	3	3	3	2	2	2	3	2	0	2	0	0	0
	<i>Galerella</i>	<i>ochracea</i>	3	3	3	3	3	3	3	3	0	3	0	0	3
	<i>Galerella</i>	<i>pulverulenta</i>	3	3	0	0	0	0	3	0	0	0	0	0	0
	<i>Galerella</i>	<i>sanguinea south</i>	3	3	0	0	0	0	3	0	0	0	0	0	0
	<i>Galerella</i>	<i>sanguinea central</i>	3	3	0	0	0	0	3	0	0	0	0	0	0
	<i>Urva</i>	<i>semitorquata</i>	3	3	3	3	3	3	3	3	0	3	0	0	3
	<i>Urva</i>	<i>smithii</i>	3	3	3	3	3	0	0	0	0	0	0	0	0
	<i>Urva</i>	<i>urva</i>	3	3	3	3	3	3	3	0	0	0	0	0	0
	<i>Urva</i>	<i>viticollata</i>	3	3	3	3	3	3	3	3	0	0	3	0	0
	<i>Ichneumia</i>	<i>albicauda</i>	3	2	0	0	2	0	3	2	0	2	0	0	0
	<i>Liberiictis</i>	<i>kuhni</i>	3	2	0	0	0	0	3	0	0	0	0	0	0
	<i>Mungos</i>	<i>gambianus</i>	3	0	0	0	0	0	3	0	0	0	0	0	0
	<i>Mungos</i>	<i>mungo</i>	3	2	0	0	0	0	3	0	0	0	0	0	0
	<i>Paracynictis</i>	<i>selousi</i>	3	3	3	0	3	0	3	0	0	0	0	0	0
	<i>Rhynchogale</i>	<i>melleri</i>	3	2	0	0	0	0	3	3	0	3	0	0	0
	<i>Suricata</i>	<i>suricata</i>	3	2	0	0	0	0	3	2	0	0	0	0	0

Family	Genus	Species	Animal	Vertebrate	Mammal	Bird	Herptile	Fish	Invertebrate	Plant	Seed	Fruit	Root	Leaf	Other Plant
HYAENIDAE	<i>Crocota</i>	<i>crocota</i>	3	3	3	0	0	0	0	0	0	0	0	0	0
	<i>Parahyaena</i>	<i>brunnea</i>	3	3	3	0	0	2	2	2	0	2	0	2	0
	<i>Hyaena</i>	<i>hyaena</i>	3	3	3	0	0	0	2	2	0	2	0	0	0
	<i>Proteles</i>	<i>cristata</i>	3	0	0	0	0	0	3	0	0	0	0	0	0
NANDINIIDAE	<i>Nandinia</i>	<i>binotata</i>	2	2	2	0	0	0	2	3	0	3	0	0	0
PRIONODONTIDAE	<i>Prionodon</i>	<i>linsang</i>	3	3	3	3	3	0	0	0	0	0	0	0	0
	<i>Prionodon</i>	<i>pardicolor</i>	3	3	2	3	2	0	0	0	0	0	0	0	0
VIVERRIDAE	<i>Arctictis</i>	<i>binturong</i>	3	3	0	2	0	3	0	2	0	2	0	2	0
	<i>Arctogalidia</i>	<i>stigmatica</i>	3	3	3	3	3	0	3	3	0	3	0	0	0
	<i>Arctogalidia</i>	<i>trivirgata</i>	3	3	3	3	3	0	3	3	0	3	0	0	0
	<i>Chrotogale</i>	<i>owstoni</i>	3	2	0	0	0	0	3	2	0	2	0	0	0
	<i>Civettictis</i>	<i>civetta</i>	3	3	3	3	3	0	3	3	0	3	0	0	3
	<i>Cynogale</i>	<i>bennettii</i>	3	3	3	3	0	3	3	3	0	3	0	0	0
	<i>Diplogale</i>	<i>hosei</i>	3	0	0	0	0	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>abyssinica</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>angolensis</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>felina</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>bourloni</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>schoutedeni</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>cristata</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>genetta</i>	3	3	3	2	0	0	2	2	0	2	0	0	0
	<i>Genetta</i>	<i>johnstoni</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>maculata</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>letabae</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>pardina</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>piscivora</i>	3	3	0	0	2	3	0	0	0	0	0	0	0
	<i>Genetta</i>	<i>poensis</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>servalina</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>thierryi</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>tigrina</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Genetta</i>	<i>victoriae</i>	3	3	3	3	3	0	3	0	0	0	0	0	0
	<i>Hemigalus</i>	<i>derbyanus</i>	3	0	0	0	0	0	3	0	0	0	0	0	0
	<i>Macrogalidia</i>	<i>musschenbroekii</i>	3	3	3	2	0	0	0	3	0	3	0	0	0
	<i>Paguma</i>	<i>larvata</i>	3	3	0	0	0	0	3	3	0	3	0	0	0
	<i>Paradoxurus</i>	<i>hermaphroditus</i>	3	3	3	0	0	0	2	3	0	3	0	0	0
	<i>Paradoxurus</i>	<i>musanga</i>	3	3	3	0	0	0	2	3	0	3	0	0	0
	<i>Paradoxurus</i>	<i>philippinensis</i>	3	3	3	0	0	0	2	3	0	3	0	0	0
	<i>Paradoxurus</i>	<i>jerdoni</i>	0	0	0	0	0	0	0	3	0	3	0	0	0
	<i>Paradoxurus</i>	<i>zeylonensis</i>	3	3	3	0	0	0	3	3	3	3	0	0	0
	<i>Poiana</i>	<i>leightoni</i>	3	3	0	3	0	0	3	3	0	3	0	0	0
	<i>Poiana</i>	<i>richardsonii</i>	3	3	0	3	0	0	3	3	0	3	0	0	0
	<i>Viverra</i>	<i>civettina</i>	3	3	3	3	3	0	3	2	0	2	2	0	0
	<i>Viverra</i>	<i>megaspila</i>	3	3	3	3	3	0	3	2	0	2	2	0	0
	<i>Viverra</i>	<i>tangalunga</i>	3	3	3	3	3	0	3	2	0	2	2	0	0
	<i>Viverra</i>	<i>zibetha</i>	3	3	3	3	3	2	3	2	0	2	2	0	0

Family	Genus	Species	Animal	Vertebrate	Mammal	Bird	Herptile	Fish	Invertebrate	Plant	Seed	Fruit	Root	Leaf	Other Plant
VIVERRIDAE	<i>Viverricula</i>	<i>indica</i>	3	3	0	0	0	0	3	3	0	3	3	0	0

Table A13-2 - Social behaviour database for Feliformia

Family	Species	Group hunting	Intragroup coalition formation	Territory Defence (Inter-group coalition)	Cooperative protection from predators	Alloparental care	Cooperation score	Source
EUPLERIDAE	<i>Cryptoprocta ferox</i>	1	0	0	0	0	1	Smith et al 2012
	<i>Cryptoprocta spelaea</i>	na	na	na	na	na	na	-
	<i>Eupleres goudotii</i>	0	0	0	0	0	0	ADW
	<i>Fossa fossana</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Galidia elegans</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Galidictis fasciata</i>	0	0	0	0	0	0	ADW
	<i>Galidictis grandidieri</i>	1	0	0	0	0	1	ADW
	<i>Mungotictis decemlineata</i>	1	0	1	0	0	2	ADW
	<i>Salanoia concolor</i>	na	na	na	na	na	na	IUCN
FELIDAE	<i>Acinonyx jubatus</i>	1	0	1	0	0	2	Smith et al 2012
	<i>Caracal aurata</i>	0	0	0	0	0	0	ADW (not much info)
	<i>Caracal caracal</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Felis chaus</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Felis margarita</i>	0	0	0	0	0	0	ADW
	<i>Felis nigripes</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Felis silvestris</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Felis bieti</i>	0	0	0	0	0	0	ADW (not much info)
	<i>Felis catus</i>	0	0	1	0	1	2	Macdonald et al 2000
	<i>Leopardus colocolo</i>	na	na	na	na	na	na	ADW
	<i>Leopardus geoffroyi</i>	0	0	0	0	0	0	ADW
	<i>Leopardus guigna</i>	0	0	0	0	0	0	ADW
	<i>Leopardus jacobita</i>	0	0	0	0	0	0	EOL
	<i>Leopardus pardalis</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Leopardus mitis</i>	0	0	0	0	0	0	Taken to be = <i>pardalis</i>
	<i>Leopardus tigrinus</i>	0	0	0	0	0	0	ADW
	<i>Leopardus guttulus</i>	0	0	0	0	0	0	Considered similar to <i>tigrinus</i>
	<i>Leopardus pardinoides</i>	0	0	0	0	0	0	considered similar to <i>tigrinus</i>
	<i>Leopardus wiedii</i>	0	0	0	0	0	0	ADW
	<i>Leptailurus serval</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Lynx canadensis</i>	1	0	0	0	0	1	ADW, Bailey et al 2013
								Bailey et al 2013 mentions apparent group hunting.; Smith et al 2012 gives score of 0;
	<i>Lynx lynx</i>	1	0	0	0	0	1	

Family	Species	Group hunting	Intragroup coalition formation	Territory Defence (Inter-group coalition)	Cooperative protection from predators	Alloparental care	Cooperation score	Source
FELIDAE	<i>Lynx pardinus</i>	0	0	0	0	0	0	ADW Bailey et al 2013 mentions apparent group hunting.; Smith et al 2012 gives score of 0;
	<i>Lynx rufus</i>	1	0	0	0	0	1	Considered same as <i>nebulosa</i>
	<i>Neofelis diardi</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Neofelis nebulosa</i>	0	0	0	0	0	0	ADW
	<i>Otocolobus manul</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Panthera leo</i>	1	1	1	1	0.5	4.5	Smith et al 2012
	<i>Panthera onca</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Panthera pardus</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Panthera tigris</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Panthera uncia</i>	1	0	0	0	0	1	Smith et al 2012
	<i>Catopuma badia</i>	0	0	0	0	0	0	ADW
	<i>Catopuma marmorata</i>	0	0	0	0	0	0	ADW
	<i>Catopuma temminckii</i>	0	0	0	0	0	0	ADW
	<i>Prionailurus bengalensis</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Prionailurus planiceps</i>	0	0	0	0	0	0	ADW
	<i>Prionailurus rubiginosus</i>	0	0	0	0	0	0	ADW
	<i>Prionailurus viverrinus</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Puma concolor</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Puma yagouaroundi</i>	0	0	0	0	0	0	ADW
HERPESTIDAE	<i>Atilax paludinosus</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Bdeogale crassicauda</i>	0	0	0	0	0	0	ADW Wiki, Gilchrist <i>et al</i> 2009
	<i>Bdeogale jacksoni</i>	0	0	0	0	0	0	ADW
	<i>Bdeogale nigripes</i>	0	0	0	0	0	0	IUCN
	<i>Bdeogale omnivora</i>	0	0	0	0	0	0	Kingdom & Hoffman, 2013
	<i>Crossarchus alexandri</i>	1	0	1	1	0	3	Kingdom & Hoffman, 2013
	<i>Crossarchus ansorgei</i>	1	0	1	1	0	3	ADW, wikipedia, Goldman (1987)
	<i>Crossarchus obscurus</i>	1	0	1	1	1	4	Wikipedia, ADW, some info based on obscurus
	<i>Crossarchus platycephalus</i>	1	0	1	1	1	4	Taylor & Meester (1993), ADW
	<i>Cynictis penicillata</i>	0	0	1	1	0	2	ADW
	<i>Dologale dybowski</i>	0	0	0	0	0	0	ADW
	<i>Helogale hirtula</i>	1	0	1	1	1	4	Smith et al 2012
	<i>Helogale parvula</i>	0	0	1	1	1	3	IUCN, 2015
	<i>Urva brachyura</i>	na	na	na	na	na	na	ADW
	<i>Urva edwardsii</i>	0	0	0	0	0	0	IUCN, 2015
	<i>Galerella flavescens</i>	na	na	na	na	na	na	

Family	Species	Group hunting	Intragroup coalition formation	Territory Defence (Inter-group coalition)	Cooperative protection from predators	Alloparental care	Cooperation score	Source
HERPESTIDAE	<i>Urva fusca</i>	na	na	na	na	na	na	Wikipedia, ADW, EOL
	<i>Herpestes ichneumon</i>	0	0	0	0	0	0	Wikipedia, ADW
	<i>Urva javanica</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Urva auropunctata</i>	0	0	0	0	0	0	Considered to be as <i>javanicus</i> Wiki, Gilchrist <i>et al</i> (2009)
	<i>Xenogale naso</i>	0	0	0	0	0	0	IUCN
	<i>Galerella ochracea</i>	0	0	0	0	0	0	IUCN
	<i>Galerella pulverulenta</i>	0	0	0	1	0	1	Smith et al 2012
	<i>Galerella sanguinea south</i>	0	0	0	0	0	0	ADW (assumed to be the same as <i>Galerella sanguinea south</i>)
	<i>Galerella sanguinea central</i>	0	0	0	0	0	0	
	<i>Urva semitorquata</i>	na	na	na	na	na	na	IUCN, 2015
	<i>Urva smithii</i>	0	0	0	0	0	0	Gilchrist et al 2009
	<i>Urva urva</i>	0	0	0	0	0	0	Wiki, Gilchrist et al 2009
	<i>Urva vitticollis</i>	0	0	0	0	0	0	Wiki, Gilchrist et al 2009
	<i>Ichneumia albicauda</i>	0	0	0	0	0	0	ADW
	<i>Liberiictis kuhni</i>	1	0	0	0	0	1	Wikipedia, Gilchrist <i>et al</i> , 2009, ADW, col
	<i>Mungos gambianus</i>	1	0	1	1	1	4	ADW
	<i>Mungos mungo</i>	1	0	1	1	1	4	Smith et al 2012; complemented with ADW
	<i>Paracynictis selousi</i>	0	0	0	0	0	0	Wikipedia
	<i>Rhynchogale melleri</i>	0	0	0	0	0	0	ADW
	<i>Suricata suricatta</i>	1	0	1	1	1	4	Smith et al 2012, Taylor & Meester (1993)
HYAENIDAE	<i>Crocota crocuta</i>	1	1	1	1	0.5	4.5	Smith et al 2012
	<i>Parahyaena brunnea</i>	0	0	1	0	1	2	Smith et al 2012, ADW
	<i>Hyaena hyaena</i>	0	0	0	0	0.5	0.5	Smith et al 2012, ADW
	<i>Proteles cristata</i>	0	0	0	0	0	0	Smith et al 2012, ADW
NANDINIIDAE	<i>Nandinia binotata</i>	0	0	0	0	0	0	ADW
PRIONODONTIDAE	<i>Prionodon linsang</i>	0	0	0	0	0	0	ADW
	<i>Prionodon pardicolor</i>	0	0	0	0	0	0	ADW
VIVERRIDAE	<i>Arctictis binturong</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Arctogalidia stigmatica</i>	na	na	na	na	na	na	Considered = <i>trivirgata</i>
	<i>Arctogalidia trivirgata</i>	na	na	na	na	na	na	ADW
	<i>Chrotogale owstoni</i>	0	0	0	0	0	0	ADW
	<i>Civettictis civetta</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Cynogale bennettii</i>	na	na	na	na	na	na	ADW
	<i>Diplogale hosei</i>	na	na	na	na	na	na	ADW

Family	Species	Group hunting	Intragroup coalition formation	Territory Defence (Inter-group coalition)	Cooperative protection from predators	Alloparental care	Cooperation score	Source
VIVERRIDAE	<i>Genetta abyssinica</i>	0	0	0	0	0	0	Gilchrist <i>et al</i> , 2009
	<i>Genetta angolensis</i>	na	na	na	na	na	na	ADW, Gilchrist <i>et al</i> , 2009
	<i>Genetta felina</i>	na	na	na	na	na	na	Wiki (<i>Genetta genetta</i> page), Gilchrist <i>et al</i> , 2009 - no info
	<i>Genetta boursloni</i>	na	na	na	na	na	na	Wiki, Gilchrist <i>et al</i> , 2009 - no info on sociality
	<i>Genetta schoutedeni</i>	na	na	na	na	na	na	Only described by Gaubert; possibly = <i>maculata</i> ?
	<i>Genetta cristata</i>	na	na	na	na	na	na	Gilchrist <i>et al</i> , 2009
	<i>Genetta genetta</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Genetta johnstoni</i>	0	0	0	0	0	0	Gilchrist <i>et al</i> , 2009
	<i>Genetta maculata</i>	0	0	0	0	0	0	Gilchrist et al 2009
	<i>Genetta letabae</i>	0	0	0	0	0	0	Only in Gaubert. Presumed ~ <i>maculata</i>
	<i>Genetta pardina</i>	na	na	na	na	na	na	Gilchrist et al 2009
	<i>Genetta piscivora</i>	0	0	0	0	0	0	ADW
	<i>Genetta poensis</i>	na	na	na	na	na	na	Gilchrist et al 2009
	<i>Genetta servalina</i>	na	na	na	na	na	na	Wiki, Gilchrist et al 2009
	<i>Genetta thierryi</i>	na	na	na	na	na	na	Wiki, Gilchrist et al 2009
	<i>Genetta tigrina</i>	0	0	0	0	0	0	Smith et al 2012
	<i>Genetta victoriae</i>	0	0	0	0	0	0	Gilchrist et al 2009
	<i>Hemigalus derbyanus</i>	0	0	0	0	0	0	ADW
	<i>Macrogalidia musschenbroekii</i>	0	0	0	0	0	0	ADW
	<i>Paguma larvata</i>	0	0	0	0	0	0	ADW
	<i>Paradoxurus hermaphroditus</i>	0	0	0	0	0	0	ADW
	<i>Paradoxurus musanga</i>	0	0	0	0	0	0	Assumed = <i>hermaphroditus</i>
	<i>Paradoxurus phillipinensis</i>	0	0	0	0	0	0	Assumed = <i>hermaphroditus</i>
	<i>Paradoxurus jerdoni</i>	0	0	0	0	0	0	ADW
	<i>Paradoxurus zeylonensis</i>	0	0	0	0	0	0	ADW
	<i>Poiana leightoni</i>							Gilchrist et al 2009; considered similar to <i>Poiana richardsonii</i>
		0	0	0	0	0	0	
	<i>Poiana richardsonii</i>	0	0	0	0	0	0	ADW
	<i>Viverra civettina</i>	0	0	0	0	0	0	Gilchrist et al 2009
	<i>Viverra megaspila</i>	0	0	0	0	0	0	Gilchrist et al 2009
	<i>Viverra tangalunga</i>	0	0	0	0	0	0	ADW
	<i>Viverra zibetha</i>	0	0	0	0	0	0	ADW
	<i>Viverricula indica</i>	0	0	0	0	0	0	ADW

References

- Bailey, I.; Myatt, J.P.; Wilson, A.M. 2013. Group hunting within the Carnivora: physiological, cognitive and environmental influences on strategy and cooperation. *Behavioural Ecology and Sociobiology* 67:1-17.
- Gilchrist, J.S.; Jennings, A.P. Veron, G.; Cavallini, P. 2009. Family Herpestidae (Mongooses) In: *Handbook of the Mammals of the World. Volume 1: Carnivores*. Wilson, D.E.; Mittermeier, R.A. (orgs) Lynx Edicions, 2009.
- Goldman, C.A. 1987. *Crossarchus obscurus*. *Mammalian Species* 290:-1.5
- IUCN, 2015. The IUCN Red List of Threatened Species. Version 2015-4. <<http://www.iucnredlist.org>>. Accessed on 10 November, 2015.
- Kingdom, J.; Hoffman, M. 2013. The Mammals of Africa V: Carnivores, Pangolins, Equids and Rhinoceroses. Bloomsbury, London, UK. pp. 328-330.
- Macdonald, D.W.; Yamaguchi, N.; Kerby, G. 2000. Group-living in the domestic cat: its sociobiology and epidemiology. In: *The Domestic Cat: The Biology of Its Behaviour*. Turner, D.C. Cambridge University Press. pp 95-118.
- Smith, J.E.; Swanson, E.M.; Reed, D.; Holekamp, K.E. 2012. Evolution of Cooperation among Mammalian Carnivores and its Relevance to Hominin Evolution. *Current Anthropology* 53(S6): S436-S452.
- Taylor, P.J.; Meester, J. 1993. *Cynictis penicillata*. *Mammalian Species* 432: 1-7.

Appendix 14 - Generation of the Diet and Sociality Distance Matrices

Dietary Distance Matrix

We used the information on Feliforms present in Kissling *et al* (2014)'s database of mammalian dietary habits as the basis for our analyses. This database attributes to each species values of 1 (preferentially consumes) to 3 (rarely consumes), or 0 (never consumes / no information) for each of 16 classes of dietary items, organised in a hierarchical structure (Animals: Invertebrates, Vertebrates: Mammals, Birds, Herpetofauna, Fish; Plants: Seeds, Fruit, Nectar, Roots, Other plant material, Leaves: Leaves from Herbaceous vegetation; Leaves from Woody/ Bushy vegetation). An analysis of Kissling *et al* (2014)'s database showed that the greater detail in dietary items used could provide more in-depth analysis of dietary similarities than those done in previous analyses of the relationship between diet and integration (Marroig & Cheverud, 2001; Goswami, 2006a), although the database could still be refined by addition of further dietary classes and a careful revision of some information, since the database was based on only two data sources (Nowak, 1999; IUCN, 2013). Due to time limitations, however, and also because diet analyses in this work were limited to the 53 taxa with better-estimated **P** matrices, information added only for some taxa absent from the original database, using data equivalent to that for closely related species (usually the species from which newly described species split)

Leopardus mitis: as *Leopardus pardalis*;

Leopardus tigrinus group: as *Leopardus tigrinus* (*L. guttulus* was considered to have the same dietary habits as *L. tigrinus*);

Galerella sanguinea group: as *Galerella sanguinea* (*G. sanguinea central* and *south* were considered to have the same dietary habits)

Arctogalidia: as *Arctogalidia trivirgata* (*Arctogalidia stigmatica* was considered to have the same dietary habits as *A. trivirgata*)

Paradoxurus musanga: as *Paradoxurus hermaphroditus*

We considered the diet of other supra-specific taxa with **P** matrices to be equal to that of one of the species within the group in question. For *Cryptoprocta*, *Crossarchus* and *Neofelis*, dietary information existed only for one species, or were the same for all species in the group. For *Prionodon*, small dietary differences exist

between *P. linsang* and *P. pardicolor* (some food items are consumed "preferentially" by *linsang*, but "often" by *pardicolor*); in this case, we considered the diet for the *Prionodon* genus to equal that of *P. linsang*.

After completing the database, three dietary items had a value of 0 (not consumed or no information) for all Feliform species for which **P** matrices have been estimated: nectar, leaves from herbaceous vegetation and leaves from woody/bushy vegetation. These dietary items were therefore removed from the final database. The full database of dietary habits is available on **Appendix 13**.

In order to produce a dietary distance matrix, the original database (with a value of 1 for "preferentially consumed" items) was reorganised in order to have crescent numerical values, so that 1 represented "rarely consumed" items and 3 represented "preferentially consumed" items. We then calculated range-normalised Manhattan Distances (equivalent to the distance used for numerical traits in Gower (1971)'s distance) for each pair of taxa:

$$\sum_{i=1}^k \frac{|a_i - b_i|}{r_i} / k,$$

where a_i and b_i are the proportions of item i in the diet of taxa a and b , r_i is the range of values in class i (maximum value - minimum value; for diet $r_i = 3$ for all i) and k is the total number of classes. All dietary categories in the database's hierarchical structure were used separately, with equal weights (following one of McNamee (2013)'s suggestions for calculating similarities using hierarchical classifications). In order to interpret the main axes of dietary variation represented by the distance matrix produced, an 'ecospace' was generated using the two first axes of a Principal Coordinate Analysis (PCO - Gower, 1966) on the dietary distance matrix (see **Appendix 8**).

Initially, other ways to use the hierarchical structure of Kissling *et al* (2014)'s database and other distance metrics to represent diet were considered and assessed with preliminary analyses. The method described above was deemed more appropriate due to producing a more adequate distribution of distances (with less abrupt breaks in the distribution), showing distinctions between taxa with relatively similar diets, allowing meaningful comparison within groups, and due to including in dietary distances effects of diet "breadth" (i.e. how generalised or specific a taxon's diet is).

A short description of all methods considered for generating the dietary distance

matrix is provided in **Appendix 15**, along with some results showing the characteristics of each method considered.

Sociality Distance Matrix

The process for generating the sociality distance matrix used as a base Smith *et al* (2012)'s classification and database. These authors classify four types of social behaviour as "present" (1) or "absent" (0): social hunting, coalition formation during intergroup contests (e.g. for territory defence), cooperative protection from predators, and intragroup coalition formation. One further social behaviour (alloparenting) is classified as "present" (1), "partially present" (0.5) or "absent". Alloparenting is classified as "partially present" when individuals share a communal den, but do not engage in true alloparental care. For more information on the definition of social behaviour types please refer to Smith *et al* (2012).

Data for species not included in Smith *et al* (2012)'s original database were obtained from various sources (ADW: <http://animaldiversity.org>; EOL: <http://eol.org>; IUCN (2015); Bailey *et al* (2013); Wikipedia; Kingdom & Hoffman (2013); Goldman (1987); Taylor & Meester (1993); Gilchist *et al* (2009)). In some cases, social behaviour characteristics present in Smith *et al* (2012)'s database were changed when information in the original database contrasted with that given in other sources. No information on social behaviour could be found for some species; these had to be removed from all analyses related to sociality. The complete database used for social behaviours is available on **Appendix 13**.

As described above for dietary distances, analyses dealing with sociality also focused on taxa with better-estimated matrices. For supra-specific taxa, we used sociality information of the species included within each group when these presented the same social behaviours (*Leopardus tigrinus* group, *Galerella sanguinea* group, *Neofelis*, *Prionodon*). For *Cryptoprocta*, we used the information available for the extant species *Cryptoprocta ferox*. For *Crossarchus*, we used the information available for *Crossarchus obscurus* and *C. platycephalus*, which are equivalent. Finally, no information on social behaviour was available for *Arctogalidia* species, so this genus was removed from sociality analyses.

After the sociality database was complete, "sociality distances" between species were calculated using range-normalised Manhattan Distances as described above for the

dietary distance matrix, using the five social behaviour classes. As done for diet, an 'ecospace' based on the sociality distance matrix was also built, using the two first axes of a Principal Coordinate Analysis (**Appendix 8**).

References

- Bailey, I.; Myatt, J.P.; Wilson, A.M. 2013. Group hunting within the Carnivora: physiological, cognitive and environmental influences on strategy and cooperation. *Behavioural Ecology and Sociobiology* 67:1-17.
- Gilchrist, J.S.; Jennings, A.P. Veron, G.; Cavallini, P. 2009. Family Herpestidae (Mongooses) In: *Handbook of the Mammals of the World. Volume 1: Carnivores*. Wilson, D.E.; Mittermeier, R.A. (orgs) Lynx Edicions, 2009.
- Goldman, C.A. 1987. *Crossarchus obscurus*. *Mammalian Species* 290:-1.5
- Goswami, A. 2006. Morphological integration in the carnivoran skull. *Evolution* 60 (1): 169-183.
- Gower, 1971. A General Coefficient of Similarity and Some of its Properties. *Biometrics* 27(4): 857-871.
- Gower, J.C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *biometrika* 53(3/4): 325-338.
- IUCN 2013. The IUCN Red List of Threatened Species. Version 2013.2.
- IUCN, 2015. The IUCN Red List of Threatened Species. Version 2015-4. <<http://www.iucnredlist.org>>. Accessed on 10 November, 2015.
- Kingdom, J.; Hoffman, M. 2013. *The Mammals of Africa V: Carnivores, Pangolins, Equids and Rhinoceroses*. Bloomsbury, London, UK.
- Kissling, W.D.; Dalby, L.; Fløjgaard, C.; Lenoir, J.; Sandel, B.; Sandom, C.; Trøjelsgaard, K.; Svenning, J.-S. 2014. Establishing macroecological trait datasets: digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecology and Evolution* 4(14): 2913-2930.
- Macdonald, D.W.; Yamaguchi, N.; Kerby, G. 2000. Group-living in the domestic cat: its sociobiology and epidemiology. In: *The Domestic Cat: The Biology of Its Behaviour*. Turner, D.C. Cambridge University Press. pp 95-118.
- Marroig, G.; Cheverud J.M.. 2001. A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology, and ontogeny during cranial evolution of new world monkeys. *Evolution* 55(12): 2576-600.
- McNamee, R.C. 2013. Can't see the forest for the leaves: Similarity and distance measures for hierarchical taxonomies with a patent classification example. *Research Policy* 42: 855-873.
- Nowak R.M. 1999. *Walker's mammals of the world. Volume 1 & 2*. Baltimore: Johns Hopkins University Press, Baltimore.
- Smith, J.E.; Swanson, E.M.; Reed, D.; Holekamp, K.E. 2012. Evolution of Cooperation among Mammalian Carnivores and its Relevance to Hominin Evolution. *Current Anthropology* 53(S6): S436-S452.
- Taylor, P.J.; Meester, J. 1993. *Cynictis penicillata*. *Mammalian Species* 432: 1-7.

Appendix 15 - Other forms considered for using the diet database to produce dietary distances.

After having the complete diet database prepared (Kissling *et al*, 2014 - see **Appendix 14**), some time was dedicated to considering which would be the best way to use it to produce a dietary distance matrix. Goswami (2006), based on the method used by Marroig & Cheverud (2001) for neotropical primates, used for her dietary comparisons in Carnivora a simple division between 4 diet categories ("carnivore", "insetivore", "frugivore" and "folivore"), associating each of these classes to the proportion of the equivalent dietary item in the composition of a species' diet, so that the sum of dietary categories for each species is 1. Dietary similarity between two taxa was then calculated as

$$\sum_{i=1}^k (a_i b_i)^{1/2}$$

where a_i and b_i are the proportions of item i in the diet of taxa a and b .

As the diet database used here has a much greater level of detail than the categorisation used by Goswami (2006), and given the hierarchical structure existent between the dietary categories in the database, different forms of representing dietary distances were explored, using distinct indexes for calculating distances and levels of detail for dietary classes.

Three different manners of using the hierarchical structure between dietary classes were tested, based on methods proposed by McNamee (2013):

- i) using distance metrics for *each* dietary category separately, using the *same weight* for each one (acronym "TF"), considering the whole hierarchical structure of dietary classes;
- ii) using distance metrics for each dietary category separately, but associating to comparisons in each category a weight corresponding to the *information content* of that category *in relation to all categories*. The weight for each dietary class is then $\log n_t / n_i$, where n_i is the frequency of dietary class i and n_t is the 'total frequency' (i.e. sum of values for all categories) - acronym "TF-IDP -Total".
- iii) as above, but the weight corresponds to the *information content* of each category *in relation to the category directly superior to it in the hierarchy* (the "parental" category): $\log n_p / n_i$, where n_p is the frequency of the parental category - acronym "TF-IDP-Parent".

These forms of using the database were compared to divisions of the dietary items available in simple, hierarchically equal "dietary categories", as done in Goswami (2006). In addition to the dietary classes used by her ("Vertebrate/ Invertebrate/ Fruit/ Leaves" - acronym used "LG" or "Goswami"), other divisions based on Kissling *et al* (2014)'s database were also tested: "Plant/Animal" (level 1);

"Plant/Vertebrate/Invertebrate" (level 2); and "Mammals/ Birds/ Herpetofauna/ Fish/ Seeds/ Fruit/ Nectar/ Roots/ Leaves/ Other plant material" (level 3).

In addition to the decision regarding how to "divide" the database for comparisons, a decision also had to be taken regarding the most appropriate distance metric to be used. The database used considers four distinct levels of consumption of each dietary item (0, 1, 2, 3; the database was reorganised so that the numbers indicated increasing importance of an item in a taxon's diet, with 3 representing "primary or frequent consumption"). The sum of all dietary categories therefore differed between taxa, and also depended on how the database was divided, as explained above. For this reason, a direct use of the similarity measure used by Marroig & Cheverud (2001) and Goswami *et al* (2006) would not be possible, since this metric is based on an assumption that the sum of dietary categories for a taxon equals 1. The metric used in these previous studies was therefore adapted in order to allow a comparison with alternative distance metrics, as described below

The following dissimilarity/distance metrics were tested:

i) Range-normalised Manhattan Distance - acronym "MD". This is equivalent to the distance used for numerical traits in Gower (1971)'s distance, and is calculated as:

$$\frac{\sum |a_i - b_i|/r_i}{k}$$

where a_i e b_i are the proportions of item i in the diet of taxa a and b , r_i is the 'range' of values in each class (in this case 3 for all classes) and k is the total number of classes;

ii) Distance between ordinal traits proposed by Podani (1999) in its "metric" version (which tends to preserve the characteristics of a "proper" distance) - acronym "MO". This distance is calculated as:

$$\frac{\sum |ra_i - rb_i|/\max r_i - \min r_i}{k}$$

where k is as described above, ra_i and rb_i are the ranks of species a and b for dietary item i , $\max r_i$ and $\min r_i$ are the maximum and minimum rank for dietary item i , respectively.

iii) Jaffe's Distance (Jaffe, 1986), corresponding to 1 - the cosine similarity between two vectors, used in McNamee (2013)'s work which was used as a base for methods to use the hierarchical structure in the dietary database - acronym DCos:

$$1 - \frac{\sum (a_i \cdot b_i)}{\sqrt{\sum a_i^2} \cdot \sqrt{\sum b_i^2}}$$

iv) A generalisation of the distance metric equivalent to the similarity measure used in Marroig & Cheverud (2001) and Goswami (2006) for cases in which the sum of dietary classes for each taxon does not equal 1 (acronym "MG" or "Gab"). This procedure is equivalent to dividing each taxon's value for each dietary category by the sum of that taxon's values for all dietary categories (i.e. converting the value in each dietary class to a proportion of the total diet):

$$1 - \frac{\sum(a_i \cdot b_i)^{1/2}}{\sqrt{\sum a_i \cdot \sum b_i}}$$

v) Dissimilarity measure used for dietary similarity in Hubbe (2013)'s work analysing morphological integration in *Xenarthra*. This measure is equivalent to the range-normalised Manhattan Distance (as in *i*), above), but attributes a distance equal to the range (3 for diet here) for all comparisons in which one (and only one) of the taxa being compared has a value of "0" for the dietary class compared (acronym "Hub" or "Alex").

An analysis of the characteristics of each set of "form of using the database" and "distance/dissimilarity" was done by assessing the distributions of pairwise distances between taxa, and the distribution of taxa in an "Ecospace" (generated using the two first axes of a Principal Coordinate Analysis - PCO on the distance/dissimilarity matrices produced in each case). A detailed discussion of the characteristics, advantages and disadvantages of each set of "database use" and "distance type" is not directly related to the objectives of this dissertation and is therefore not done here. The ecospace for the pairwise distances obtained with each set of database use and distance type are shown in **Figures A15-1 to A15-5**; the distributions of pairwise distances are shown in **Figure A15-6**. Ecospace corresponding to analyses using the "level 1" database use type (plants and animals only) are not shown, as they correspond to one-dimensional spaces with "strict carnivores" on one side and "strict herbivores" on the opposite end.

After these preliminary analyses, some sets of "database use" ("TF", "TF-IDP Total" and "LG") and "distance type" ("MD", "MG/Gab" and "Hub") were tentatively used for comparisons with similarities in integration patterns and magnitudes and other factors (see **Table A15-1** for an example, using the 50 *Feliformia* species with better-estimated matrices and information on social behaviour). Due to the greater level of detail preserved in the ecospace and the relatively appropriate distribution of pairwise distances with the hierarchical use of the database with equal weights ("TF") and the range-normalised Manhattan Distance ("MD"), this set of database use and distance metric was chosen for use in all analyses performed for this dissertation.

Figure A15-1. Ecospace produced with different database use methods coupled with the "Alex/Hub" dissimilarity measure. The Figure with "Level 1" actually shows the results for the "Level 2" database use ("Plant/Vertebrate"/"Invertebrate").

Figure A15-2. Ecospace produced with different database use methods coupled with the "MG/Gab" distance.
The Figure with "Level 1" actually shows the results for the "Level 2 " database use ("Plant/Vertebrate/"Invertebrate").

Figure A15-3. Ecospace produced with different database use methods coupled with the Jaffe ("Dcos") distance. The Figure with "Level 1" actually shows the results for the "Level 2 " database use ("Plant/Vertebrate/"Invertebrate").

Figure A15-4. Ecospace produced with different database use methods coupled with range-normalised Manhattan distance ("MD"). The Figure with "Level 1" actually shows the results for the "Level 2" database use ("Plant/Vertebrate"/"Invertebrate").

Figure A15-5. Ecospace produced with different database use methods coupled with the "metric" Rank distance ("MO") proposed by Podani (1999). The Figure with "Level 1" actually shows the results for the "Level 2" database use ("Plant/Vertebrate/"Invertebrate").

Figure A15-6. Pairwise distance distributions (between all Feliformia species) produced with different sets of 'database use' and 'distance/dissimilarity metric'. For the "MG/Gab" and "DCos"/Jaffe's distances, there are in all cases a few pairwise comparisons with a distance of 1, corresponding to cases in which the species compared share no dietary category. As these comparisons occur in relatively small numbers, they are not readily visible in the histograms.

Table A15-1. Example of a table with Mantel Test results including different "database use" ("TF", "TF-IDP Total" and "LG") and "distance metric" ("MD", "MG/Gab", "Hub/Alex") sets for Feliformia, including the 50 taxa with better-estimated matrices and available information on social behaviour.

50 taxa		Diet							Phylogeny		Sociality	Morpho	Pattern	Magnitude	Size
		MD TF	MD TF-IDP Total	MG TF	Hub TF	MD LG	MG LG	Hub LG	Branch	Nodes	data	Mahal.	RS	r ²	ln (gm)
Diet	MD TF														
	MD TF-IDP Total	0.962													
	MG TF	0.846	0.734												
	Hub TF	0.959	0.948	0.805											
	MD LG	0.746	0.705	0.756	0.750										
	MG LG	0.530	0.436	0.751	0.527	0.839									
	Hub LG	0.681	0.678	0.667	0.755	0.952	0.788								
Phylogeny	Branch	0.377	0.314	0.418	0.366	0.532	0.502	0.480							
	Nodes	0.152	0.094	0.149	0.140	0.222	0.212	0.180	0.582						
Sociality	data	-0.027	-0.061	0.057	-0.032	0.017	-0.030	0.000	-0.006	0.012					
Morphology	Mahal.	0.107	0.123	0.181	0.156	0.231	0.217	0.260	0.329	0.064	0.334				
Pattern	RS	0.158	0.129	0.249	0.172	0.270	0.281	0.251	0.431	0.083	0.081	0.334			
Magnitude	r ²	0.006	-0.017	0.066	0.020	0.079	0.141	0.060	0.253	0.092	0.104	0.253	0.339		
Size	ln (gm)	0.003	-0.027	0.105	0.021	0.075	0.064	0.077	0.156	0.038	0.322	0.775	0.259	0.194	
Size variation	isovar	0.058	0.029	0.113	0.068	0.130	0.164	0.106	0.323	0.099	0.060	0.198	0.548	0.896	0.158

References

- Goswami, A. 2006. Morphological integration in the carnivoran skull. *Evolution* 60 (1): 169-183.
- Gower, 1971. A General Coefficient of Similarity and Some of its Properties. *Biometrics* 27(4): 857-871.
- Hubbe, A. 2013. Análise morfológica craniana de Xenarthra atuais e extintos: inferências evolutivas e funcionais. Doctoral dissertation, Universidade de São Paulo.
- Jaffe, A. 1986. Technological opportunity and spillovers of R & D: Evidence from firms' patents, profits and market value. *The American Economic Review* 76(5): 984-1001.
- Kissling, W.D.; Dalby, L.; Fløjgaard, C.; Lenoir, J.; Sandel, B.; Sandom, C.; Trøjelsgaard, K.; Svenning, J.-S. 2014. Establishing macroecological trait datasets: digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. *Ecology and Evolution* 4(14): 2913-2930.
- Marroig, G.; Cheverud J.M.. 2001. A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology, and ontogeny during cranial evolution of new world monkeys. *Evolution* 55(12): 2576–600.
- McNamee, R.C. 2013. Can't see the forest for the leaves: Similarity and distance measures for hierarchical taxonomies with a patent classification example. *Research Policy* 42: 855-873.
- Podani, J. 1999. Extending Gower's General Coefficient of Similarity to Ordinal Characters. *Taxon* 48(2): 331-340.

Appendix 16 - Assessment on the use of alternative comparative methods (PGLS, D-PGLS) and techniques to identify phylogenetic signal (K test, K-mult) for studying the evolution of integration in Feliformia.

Rationale - why use alternative Comparative Methods and Tests for Phylogenetic Signal?

As morphological integration patterns, phylogeny and ecological traits are usually represented as similarity/distance matrices, Mantel tests (Mantel, 1967) have traditionally been the method of choice in morphological integration studies to assess the influence of phylogenetic history (i.e. phylogenetic signal - e.g. Marroig & Cheverud, 2001; Goswami, 2006; Porto *et al*, 2009; Oliveira *et al*, 2009) and correlations between traits (e.g. integration patterns and diet or morphology - e.g. Marroig & Cheverud, 2001; Goswami, 2006; Oliveira *et al*, 2009) before or after controlling for phylogenetic relatedness. The latter case corresponds to phylogenetic comparative analyses, and usually employed partial Mantel tests (Smouse *et al*, 1986; Legendre, 2000). Recently, the use of Mantel Tests has been the target of heavy criticism, due both to generally inflated type-II errors (Legendre, 2000; Harmon & Glor, 2010) and to inflated type-I error in common partial Mantel tests (Oden & Sokal, 1992; Lapointe & Legendre, 1995; Harmon & Glor, 2010; Guillot & Rousset, 2013).

Although low power (inflated type-II errors) seems to be a general, unavoidable feature of Mantel tests (Legendre, 2000) - which led some to recommend their use only when data must necessarily be represented as distance matrices - Harmon & Glor (2010) showed that type-I error rates when using Mantel Tests for testing phylogenetic signal are equivalent to those for other well-established methods (K test - Blomberg *et al*, 2003). Harmon & Glor (2010) also show that inflated type-I error rates for comparative analyses using partial Mantel Tests can be circumvented by exchanging the usual random permutations of matrix rows and columns of traditional Mantel tests for a method of phylogenetic permutations (Lapointe & Garland, 2001). Although this might arguably justify continued use of Mantel Tests (with phylogenetic permutations when used as comparative methods) for morphological integration analyses, their low power and the potential confusion arising from disagreements between Mantel Tests and Pearson's correlation on raw data (due to their different formulations and objectives; Dutilleul *et al*, 2000) are good reason to look into alternative methods to detect

phylogenetic signal and perform comparative analyses and compare their results to those of the traditionally used Mantel Tests.

Tests for Phylogenetic Signal and Comparative Methods for univariate response variables have now been available for a relatively long time (e.g. K test - Blomberg *et al*, 2003; Phylogenetic Regression - PGLS, Grafen, 1989; Martins & Hansen, 1997; PGLS _{λ} Freckleton *et al*, 2002; Revell, 2010), and may be easily used to analyse traits like body size and integration magnitude (represented by a single value such as the mean coefficient of determination, r^2 - van Valen, 1974) . The use of these methods for multivariate traits is also possible, but their power depends on the proportion between the number of trait dimensions (p) and the number of species in the phylogeny (N); when $p \geq N$, their use is rendered impossible (Adams 2014 a,b). More recently, new methods have been proposed that allow the extension of tests of Phylogenetic Signal and Phylogenetic Comparative Methods to arbitrarily high-dimensional response variables (K-mult: Adams, 2014a; D-PGLS, Adams, 2014b). Provided distance- or similarity-based traits (i.e. integration patterns, ecological features) are first transformed to multivariate sets (e.g. using Principal Coordinate Analysis -PCoA, Gower, 1966), it is therefore now possible to use alternative tests for detecting phylogenetic signal and comparative methods and contrast their results to those of traditional Mantel Tests, assessing whether the results agree between methods and, if not, what the differences in results might imply.

Here we tested for Phylogenetic Signal in 6 factors (integration patterns and magnitudes, average morphology, size, diet and social behaviour) within Feliformia and the family Herpestidae using the K-test (Blomberg *et al*, 2003) and its multivariate extension (K-mult - Adams, 2014a) and briefly compare the results to those obtained using Mantel Tests to test for Phylogenetic Signal in **Chapter 2**. We also assessed the relationships between the 6 factors mentioned above in Feliformia and Herpestidae using PGLS _{λ} (Freckleton *et al*, 2002; Revell, 2010) and multivariate D-PGLS (Adams, 2014b) and provide a brief comparison to the results using partial Mantel Tests with Phylogenetic Comparisons (Lapointe & Garland, 2001; Harmon & Glor, 2010 - **Chapter 2**). This short assessment thus provides a first assessment of the implications of using different methods when accounting for phylogenetic history in studies of the evolution of integration.

Materials and Methods

K and K-mult tests, PGLS, D-PGLS and Permutational (M)ANOVAs were performed for Feliformia as a whole, using the 50 taxa with better-estimated **P** matrices and available information on sociality, and also for Herpestidae, using 9 taxa with well-estimated **P** matrices. The phylogenetic hypothesis used is shown in **Appendix 12**. To allow the use of K-tests, Kmult, PGLS_λ and D-PGLS, all traits originally represented by similarity (integration patterns) or distance matrices (average morphology, diet and sociality - see **Chapter 2** and **Appendix 14**) were converted to species-by-"variable" matrices by performing a Principal Coordinate Analysis (Gower, 1966) on distance/dissimilarity matrices, using the set of scores for "variables" with positive associated eigenvalues as multivariate representations of each trait. For Integration Patterns, we converted the Random Skewers similarity matrix (IPSM) to an approximately-Euclidean distance prior to the Principal Coordinate Analysis, as this increases the number of positive eigenvalues, and consequently the level of detail available for analyses. To do this, we limited adjusted pairwise similarities with values >1 on IPSM to 1, then calculated $\sqrt{(1 - IPSM)}$ (Gower & Legendre, 1986). This allowed the use of 44 "variables" associated to positive eigenvalues to represent the multivariate character "integration patterns".

For originally univariate characters (skull Size, represented by the logarithm of the geometric mean of the 35 linear measurements used as characters - log gm; and integration magnitude, represented by r^2), we used the K test (Blomberg *et al*, 2003) to measure phylogenetic signal and test its significance. Comparative analyses relating Skull Size and r^2 to Integration Patterns, Average Morphology, Diet and Sociality used PGLS with simultaneous optimisation of the phylogenetic signal (λ - Pagel, 1999) of the residuals of the dependent variable (Freckleton *et al*, 2002; Revell, 2010 - PGLS_λ).

For multivariate characters resulting from Principal Coordinate Analyses (Integration Patterns, Average Morphology, Diet and Sociality), we used Kmult (Adams, 2014a) to measure and test the significance of phylogenetic signal, and D-PGLS (Adams, 2014b) to perform Phylogenetic Comparative analyses. Phylogenetic signal in model residuals cannot be simultaneously estimated with D-PGLS, as this method is currently limited to a formulation under a Brownian Motion model of evolution (i.e. $\lambda=1$ in model residuals). This poses a potential problem, since the presence of Phylogenetic Signal on either the predictor, the response variable or on both

variables does not necessarily mean that a Phylogenetic Regression should be used instead of an ordinary least-squares regression (Revell, 2010), and so neither does it necessarily justify using a Brownian Motion model for the residuals of the dependent variable. When presenting the D-PGLS method, Adams (2014b) circumvents this by comparing the significance and goodness of fit (R^2) of D-PGLS, standard multivariate regression and an ANOVA with two phylogenetic groups as factors. Here we use a similar approach, comparing Integration Patterns, Average Morphology, Diet and Sociality among themselves and with r^2 and Size by performing D-PGLS (i.e. Phylogenetic analyses, λ in residuals=1) and Permutational MANOVAs (i.e. non-phylogenetic analyses, λ in residuals=0) and comparing the results to Permutational MANOVAs based on taxonomic groups: "families", "subfamilies" and "genera" (for Feliformia), or "subfamilies" (for Herpestidae). As in our case D-PGLS and Permutational MANOVAs have differing numbers of independent variables, direct comparisons using R^2 values are not justified, since an increase in the number of predictors necessary leads to higher R^2 values. For this reason, we compared the results of different analyses using adjusted R^2 values, calculated according to Fisher's formula (R^2_{adj} - Fisher, 1924; Anderson, 2003), which penalises R^2 values according to the number of independent variables in the model:

$$R^2_{adj} = 1 - (1 - R^2) \cdot \frac{n - 1}{n - p - 1}$$

where R^2 is the raw goodness of fit calculated for each analysis, n is the sample size (number of taxa) and p is the number of independent variables in the model. In some cases, the number of variables used to represent multivariate traits had to be reduced for the Permutational ANOVAs and D-PGLS tests; these are indicated in the results.

K-tests were performed using the R functions "phylosig" (package "phytools", Revell, 2012). K-mult tests used the R function "test.K.mult" provided in Adams (2014a). PGLS $_{\lambda}$ used the R function "pgls" (package "caper", Orme *et al*, 2013). D-PGLS used the R function "D.pgls" provided in Adams (2014b). Permutational ANOVAs used the R function "adonis" (package "vegan", Oksanen *et al*, 2015).

Results

Table A16-1 shows the results of tests for Phylogenetic Signal using Blomberg's K and Adams (2014)'s Kmult. For Feliformia as a whole, only sociality shows no phylogenetic signal, while for Herpestidae a significant phylogenetic signal is found for

sociality and average morphology, as well as for diet at $\alpha = 0.10$). These results strictly agree with those for Mantel Tests (**Chapter 2, Table 2.3**) in regard to significance for Feliformia. For Herpestidae, most results also show an agreement with those of Mantel Tests, although some differences do occur: diet is significant at $\alpha=0.05$ for Mantel but only at $\alpha=0.10$ for Kmult; and morphology shows significant phylogenetic signal for Kmult, but not for Mantel.

Although a significant positive correlation between the absolute value of Mantel Correlations and K/Kmult also exists for Herpestidae, little agreement is found between the absolute values found with both methods for Feliformia (**Figure A16-1**). For example, the correlation between Phylogeny and Integration Patterns for Feliformia is the highest according to Mantel Tests, while Integration Patterns show the lowest significant Phylogenetic Signal according to the Kmult test.

Figure A16-1. Correlation between absolute values of Mantel Correlations (mant, x axis) and K/Kmult (K, y axis) when testing for Phylogenetic Signal in Feliformia (A; $r = -0.09$, $p = 0.86$) and Herpestidae (B; $r = 0.87$, $p = 0.23$).

The results of comparative analyses using PGLS and D-PGLS/Permutational ANOVAs are shown in **Tables A16-2** (Permutational ANOVAs for taxonomic groupings), **A16-3** (PGLS/D-PGLS for Feliformia) and **A16-4** (PGLS/D-PGLS for Herpestidae). As seen in **Table A16-2**, differences between subfamilies are those that best explain variation in Integration Magnitudes ($R^2_{adj} = 55.34\%$) and Sociality (33.41%). For Integration Patterns, differences between families are almost as informative as those for subfamilies ($R^2_{adj} = 18.99\%$ for families and 21.06% for

subfamilies). Differences between genera have the best explanatory power for variations in Size ($R^2_{adj} = 77.75\%$) and Diet ($R^2_{adj} = 64.47\%$); for Size, subfamilies are almost equally informative ($R^2_{adj} = 74.74\%$). Average Morphology is equally well explained by differences between subfamilies (70.94%) and genera (69.52%). For Herpestidae, differences between the two subfamilies are only significant for Morphology ($R^2_{adj} = 31.82\%$).

Table A16-1. Phylogenetic signal (Blomberg's K, or its multivariate equivalent Kmult - Adams, 2014a) in Patterns (IP) and Magnitudes (r^2) of Integration, Morphology (Mahalanobis Distance - MD), Size (log gm), Diet and Sociality for Feliformia as a whole and for the family Herpestidae. Significance indicated by underlined values in **boldface** ($\alpha=0.05$) and *italic* ($\alpha=0.10$). p= number of variables used to represent each trait.

		Pattern (IP)	Magnitude (r^2)	Morphology (MD)	Size	Diet	Social
Feliformia	K / Kmult	0.191	0.271	0.476	0.661	0.272	0.180
n=50	P	44	1	41	1	21	26
Herpestidae	K / Kmult	0.824	0.618	1.027	1.012	<i>1.025</i>	1.765
n=9	P	8	1	8	1	4	1

The PGLS analysis for Feliformia shows significant regressions of Integration Pattern and average Morphology on Magnitudes of Integration (r^2 - **Table A16-3A**). ML estimation for regressions on r^2 incorporates very high Phylogenetic Signal for Pattern ($\lambda=1.023$), but none ($\lambda=0$) for average Morphology, despite the presence of phylogenetic signal for r^2 , Integration Patterns and average Morphology. Body size is not recognised as a significant predictor of r^2 (with a ML estimation of $\lambda=0.462$). PGLS analyses also show that average Morphology, Integration Patterns and Magnitudes are significant predictors of Body Size, with very high Phylogenetic Signal incorporated on the regression for Integration Patterns and Magnitudes ($\lambda=1.023$ and 1.012, respectively), but none ($\lambda=0$) for average Morphology.

D-PGLS ($\lambda=1$) for Feliformia (**Table A16-3B**) also shows significant regressions of r^2 and average Morphology on Integration Patterns; the same results are obtained with a non-phylogenetic regression ($\lambda=0$), with a slightly higher proportion of variance explained. Size is a significant predictor of integration patterns for $\lambda=0$ or $\lambda=1$ (for $\alpha = 0.10$ in the second case), although it explains a low proportion of variance in both cases ($R^2_{adj} = 7.04\%$ and 3.99% for $\lambda=0$ and $\lambda=1$, respectively). Phylogenetic regressions (D-PGLS) on average Morphology, on the other hand, show significance

only for Size, while non-phylogenetic regressions ($\lambda=0$) on average morphology are also significant for Integration Patterns, r^2 and Diet. In all cases except for average morphology as a predictor of integration patterns (with $\lambda=0$ or 1), taxonomic divisions (**Table A16-2**) explain a higher proportion of total variance than regressions between these factors.

These results at least partially agree with those obtained with Mantel Tests (**Chapter 2, Table 2.3**) indicating an association of body size, average morphology, integration patterns and magnitude in Feliformia, although there are some noticeable differences. For these four factors, the differences mostly relate to the "directionality" of relationships recognisable in regression models, but not in Mantel Correlations. For example, body size is predicted well by r^2 , Integration Patterns and average morphology, but is itself a good predictor only for morphology. Contrarily, average morphology seems to be a good predictor of r^2 and Integration Patterns, but is not necessarily predicted particularly well by them (at least if considering $\lambda=1$).

Table A16-2. Results of permutational Analyses of Variance by taxonomic groupings for Integration Patterns and Magnitudes (r^2), Morphology (Mahalanobis Distance - MD), Size (log gm), Diet and Sociality for Feliformia as a whole and for the family Herpestidae. The table shows Adjusted R^2 values; significance is indicated by *italic* ($p<0.10$) or **boldface** ($p<0.05$). p = number of variables used to represent each trait.

Feliformia (n=50)	Pattern	r^2	Morphology	Size	Diet	Social
Families (k=7)	18.99%	42.02%	48.90%	46.78%	20.85%	10.57%
Subfamilies (k=14)	21.06%	55.34%	70.94%	74.74%	37.12%	33.41%
Genera (k=37)	9.93%	21.62%	69.52%	77.75%	64.47%	26.35%
p	44	1	41	1	21	26

Herpestidae (n=9)	Pattern	r^2	Morphology	Size	Diet	Social
Subfamilies (1)	15.61%	0.05%	31.82%	27.68%	8.64%	30.77%
p	8	1	8	1	4	1

Table A16-3 - Alternative phylogenetic comparative analyses for Feliformia. (A) PGLS (univariate), indicating Maximum Likelihood estimate for λ , probability of $\lambda=0$ or $\lambda=1$ and adjusted R^2 . (B) D-PGLS (multivariate), indicating adjusted R^2 for $\lambda=0$ (Permutational ANOVA) and $\lambda=1$. Significance is indicated in *italic* ($\alpha < 0.10$) or **boldface** ($\alpha < 0.05$). Underlined values indicate equivalence to the ML estimate (A) or greater variance explained than the taxonomic groupings in **Table A16.2** (B). p= number of variables effectively used to represent the trait for each analysis.

Feliformia (n=50)		ML estimate		$\lambda = 0$ (No Signal)		$\lambda = 1$ (BM)	
A - PGLS (univariate)		λ	adj R^2	P($\lambda = 0$)	adj R^2	P($\lambda = 1$)	adj R^2
r ²	Pattern	<u>1.023</u>	99.92%	<0.0001	90.88%	<0.0001	93.41%
	Morph (p=37)	0.000	<u>57.78%</u>	1.0000	<u>57.78%</u>	0.0012	53.43%
	Size	0.462	4.80%	<0.0001	14.80%	<0.0001	14.23%
	Diet (p=13)	0.000	37.71%	1.0000	<u>37.71%</u>	<0.0001	9.51%
	Social (p=5)	0.461	0.00%	<0.0001	1.26%	<0.0001	0.00%
Size	Pattern	<u>1.023</u>	94.27%	<0.0001	64.86%	<0.0001	53.47%
	r ²	<u>1.012</u>	20.04%	<0.0001	14.80%	<u>0.6389</u>	14.23%
	Morph (p=37)	0.000	99.33%	1.0000	99.33%	<0.000	98.18%
	Diet (p=13)	0.956	0.00%	<0.0001	31.99%	<u>0.3807</u>	<u>0.01%</u>
	Social (p=5)	0.929	<u>15.40%</u>	<0.0001	36.58%	0.0697	14.23%

B - D-PGLS (multivariate)							
		$\lambda = 0$	$\lambda = 1$			$\lambda = 0$	$\lambda = 1$
Pattern (p = 44)	r ²	14.09%	10.86%	Diet (p = 21)	Pattern	30.99%	49.83%
	Morphology	<u>24.45%</u>	<u>55.12%</u>		r ²	10.99%	7.18%
	Size	7.04%	3.99%		Morphology	15.96%	28.82%
	Diet	12.89%	36.18%		Size	6.14%	3.71%
	Social	2.52%	54.01%		Social	0.00%	32.00%
Morphology (p = 41)	Pattern	64.79%	62.06%	Social (p = 26)	Pattern	42.82%	66.92%
	r ²	13.18%	8.71%		r ²	1.85%	2.14%
	Size	48.49%	37.74%		Morphology	<u>62.48%</u>	<u>77.65%</u>
	Diet	59.63%	12.09%		Size	2.11%	8.89%
	Social	14.80%	37.29%		Diet	0.00%	38.09%

Diet is also recognised as a significant predictor of Integration Patterns and average Morphology for non-phylogenetic analyses ($\lambda=0$), but not for phylogenetic regressions ($\lambda=1$) within Feliformia (**Table A16-3B**). These results are also akin to those for Mantel Tests, where Diet correlates to Integration Patterns and average Morphology only before correcting for phylogenetic relatedness (**Chapter 2, Table 2.3**). Unlike Mantel Tests results, however, Diet is also identified as a significant predictor of r^2 using PGLS. The ML estimation indicates that no phylogenetic information should be incorporated to the regression in this case (estimated $\lambda=0$). In all cases, permutational MANOVAs using taxonomic groupings as factors explain a higher

amount of variation than Diet does (**Table A16-2**). Diet itself is significantly predicted only by non-phylogenetic regressions of r^2 and Size ($\lambda=0$), and these factors explain a minor amount of total dietary variation.

Sociality is identified as a significant predictor only for Size (i.e. not for average Morphology), explaining a relatively small amount of total variation (15.40%) after accounting for phylogenetic signal (ML $\lambda=0.929$). Size likewise works as a significant predictor for Sociality (with $\lambda=1$, but not $\lambda=0$), but also explains a minor amount of variation in social behaviour (8.89%). Average Morphology, on the other hand, is a very good predictor of sociality; the regression of average Morphology on Sociality is significant, and explains a greater amount of variation than the permutational MANOVA using subfamilies, with or without incorporating phylogenetic signal ($\lambda=0$ or 1). Once again, these results partially mirror those for Mantel Tests, where Sociality is significantly correlated to Size and Morphology.

For Herpestidae (**Table A16-4**), Integration Patterns and Diet are found as significant predictors of Integration Magnitudes (r^2), with a very high phylogenetic signal incorporated in the regression in both cases ($\lambda=1.730$), differing from Mantel Tests, which indicate no correlation of r^2 to any other factors for this family. Integration Patterns, on the other hand, are significantly predicted only by Diet and Sociality (at $\alpha=0.10$) with non-phylogenetic regressions ($\lambda=0$). As the Permutational ANOVA using subfamilies is not significant for Integration Patterns and no phylogenetic signal for Integration Patterns was recognised for Herpestidae, it is possible that a non-phylogenetic regression might be the most appropriate in this case, implying that Diet and Sociality indeed significantly affect Integration Patterns for mongooses - as indicated by Mantel Test results.

Table A16-4 - Alternative phylogenetic comparative analyses for Herpestidae. (A) PGLS (univariate), indicating Maximum Likelihood estimate for λ , probability of $\lambda = 0$ or $\lambda = 1$ and adjusted R^2 . (B) D-PGLS (multivariate), indicating adjusted R^2 for $\lambda = 0$ (Permutational ANOVA) and $\lambda = 1$. Significance is indicated in *italic* ($\alpha < 0.10$) or **boldface** ($\alpha < 0.05$). Underlined values indicate equivalence to the ML estimate (A) or greater variance explained than the taxonomic groupings in **Table A16.2** (B). p= number of variables effectively used to represent the trait for each analysis.

Herpestidae (n=9)		ML estimate		$\lambda = 0$ (No Signal)		$\lambda = 1$ (BM)	
A - PGLS (univariate)		λ	adj R^2	P($\lambda = 0$)	adj R^2	P($\lambda = 1$)	adj R^2
r ²	Pattern (p=7)	1.730	<u>99.57%</u>	0.0007	<u>62.36%</u>	0.0002	77.85%
	Morph (p=6)	0.000	0.00%	1.0000	0.00%	0.0599	0.00%
	Size	0.000	1.67%	1.0000	1.67%	0.0483	0.92%
	Diet	1.730	<u>99.05%</u>	0.0194	38.65%	0.0216	60.74%
	Social	0.000	3.78%	1.0000	3.78%	0.0447	1.64%
Size	Pattern (p=7)	1.730	<u>99.92%</u>	0.0041	87.82%	0.0069	88.72%
	r ²	<u>0.643</u>	1.14%	<u>0.5458</u>	1.67%	<u>0.6652</u>	0.92%
	Morph (p=7)	<u>1.730</u>	96.79%	0.0151	0.00%	0.0126	0.00%
	Diet	1.730	<u>99.55%</u>	1.0000	<u>53.91%</u>	0.0301	49.69%
	Social	1.730	<u>99.12%</u>	1.0000	9.86%	0.0288	1.11%
Social	Pattern (p=7)	1.730	<u>99.86%</u>	1.0000	<u>97.78%</u>	0.0163	95.89%
	r ²	<u>0.022</u>	3.78%	<u>0.9773</u>	3.78%	<u>0.1687</u>	1.64%
	Morph (p=7)	0.000	94.89%	1.0000	94.89%	<u>0.1946</u>	<u>89.53%</u>
	Size	0.000	9.86%	1.0000	9.86%	<u>0.1117</u>	1.11%
	Diet	1.730	<u>97.59%</u>	0.0037	44.75%	0.0072	18.02%

B - D-PGLS (multivariate)		$\lambda = 0$	$\lambda = 1$			$\lambda = 0$	$\lambda = 1$
Pattern	r ²	14.50%	19.20%	Diet	Pattern (p=7)	74.66%	71.31%
(p =8)	Morphology (p=7)	0.00%	9.16%	(p = 4)	r ²	16.68%	26.87%
	Size	9.93%	10.91%		Morphology (p=7)	<u>95.29%</u>	<u>94.09%</u>
	Diet	<u>12.68%</u>	16.80%		Size	20.01%	18.58%
	Social	<u>16.16%</u>	17.02%		Social	<u>29.89%</u>	11.54%
Morphology	Pattern (p=7)	64.53%	66.60%				
(p = 8)	r ²	3.88%	5.45%				
	Size	<u>51.54%</u>	<u>45.92%</u>				
	Diet	30.63%	17.07%				
	Social	18.52%	9.45%				

Size is the only significant predictor found for average Morphology, with phylogenetic and non-phylogenetic regressions (explaining 45.92% and 51.54% of variation with $\lambda=1$ and $\lambda=0$, respectively), while average Morphology is itself a significant predictor of Diet only (with $\lambda=1$ and $\lambda=0$, explaining a high proportion of dietary variance in both cases). Body size does not act as a significant predictor of any other factor for Herpestidae, but is itself predicted significantly well by Integration

Patterns, Diet and Sociality (but not by average Morphology, despite a very high R^2_{adj}), all with very high ML estimates of λ ($\lambda=1.73$). Integration Patterns and Diet are found to be significant predictors for Social Behaviour within Herpestidae, in both cases also with very high λ estimates (a PGLS was used for phylogenetic regressions on Sociality for mongooses, as this factor is adequately represented by a single 'variable' for this group). Finally, significant predictors of Diet identified for Herpestidae were average Morphology (with $\lambda=0$ or $\lambda=1$) and Sociality (only for non-phylogenetic regressions, $\lambda=0$).

Although ML estimates of λ were limited to values which did not produce negative branch lengths, PGLSs with very high λ estimates have usually shown very high R^2_{adj} . It is unclear whether these results represent real phenomena (implying shared variation between predictors, since $\sum adjR^2$ for different predictors $> 100\%$) or artefacts (perhaps due to low species sample size; coincident high λ and R^2_{adj} were found more often for Herpestidae with $n=9$).

Discussion

The results obtained with alternative approaches used for testing Phylogenetic Signal (K/Kmult) and for Phylogenetic Comparative Methods (PGLS/D-PGLS) agree in great part with those found using Mantel Tests (**Chapter 2 - Table 2.3**). This general concurrence in results indicates that the use of Mantel Tests and partial Mantel Tests with Phylogenetic Permutations (Harmon & Glor, 2010) for Phylogenetic Comparative Analyses is generally justified, and that harsher general criticism of Mantel Tests such as that levied by Guillot *et al* (2013) may be somewhat exaggerated.

Tests for Phylogenetic Signal show equivalent results with K/Kmult and Mantel for Feliformia; one difference is that, in Herpestidae, a significant Phylogenetic Signal is recognised for Sociality with both methods, while average Morphology and Diet show Phylogenetic Signal for Kmult only. This disparity, with significant Phylogenetic Signal being recognised for some factors with Kmult, but not Mantel Tests, seems to agree with previous comments that the latter tend to have lower power (i.e. higher type II error) than alternative methods (Legendre, 2000; Harmon & Glor, 2010). On the other hand, a significant positive correlation between Mantel Correlations and K/Kmult values is found for Herpestidae, but not for Feliformia. The reason for this difference is not so clear; it may be related to the fact that Matrix Correlations and the K metric of

Bloomberg *et al* (2003) in fact measure different (albeit related) things, as stated by Dutilleul *et al* (2000). However, it seems warranted to perform more detailed future investigations on the circumstances in which these methods produce different results, as well as on how exactly to interpret the values of Matrix Correlations in the context of Phylogenetic Signal.

The results of comparative phylogenetic analyses using PGLS/D-PGLS are also in large part in agreement with those of Mantel Tests, especially for Feliformia as a whole (for which species sample size = 50). One important difference is that PGLS/D-PGLS, being based on regression models, identifies "non-parallel" relationships between factors (i.e. x as a good predictor of y , but not the opposite), while Mantel Tests simply inform whether two variables are correlated. If significant relations between factors in either direction for PGLS/D-PGLS are considered to correspond to a significant correlation for Mantel Tests, the agreement between PGLS/D-PGLS and Mantel Tests is almost complete for Feliformia. The only two differences are that PGLS/D-PGLS recognise links between Diet and Integration Magnitudes (r^2), as well as identifying Size as a significant predictor of Dietary habit. As mentioned above for Phylogenetic Signal, these differences might indicate a higher power of alternative comparative methods in comparison to Mantel Tests, as argued by Legendre (2000) and Harmon & Glor (2010).

Differences between Mantel Tests and PGLS/D-PGLS for Herpestidae, on the other hand, appear to be larger. While the majority of results still agree between both tests, relationships between variables were identified in four instances using PGLS/D-PGLS, but not Mantel Tests: this was the case for Integration Patterns as a significant predictor of r^2 and Body Size, for Diet as a significant predictor of r^2 , and also for Sociality as a significant predictor of Body Size. Additionally, relationships between Diet and Sociality were identified with both phylogenetic and non-phylogenetic regressions with D-PGLS, but only after correcting for Phylogeny with Mantel Tests. Similarly, Diet was identified as a significant predictor of Integration Patterns only with non-phylogenetic regressions, while Mantel Tests identified a link between these factors only after correcting for Phylogenetic Relatedness. Finally, a link between average Morphology and Sociality within Herpestidae was identified with Mantel Tests (before and after correcting for Phylogeny), but not with PGLS/D-PGLS. Therefore, while most differences between methods for Herpestidae may also be accounted for by the lower

power of Mantel Tests, there were at least some cases in which PGLS/D-PGLS did not recognise correlations identified as significant by Mantel Tests.

On the one hand, the high agreement in results between Mantel Tests and PGLS/D-PGLS is encouraging, as it provides greater support to coincident results, as well as seeming to indicate that previous results obtained using Mantel Tests for testing Phylogenetic Signal and for Comparative Phylogenetic Analyses tend to be at least somewhat reliable - apparently especially so when species sample size is relatively large as in the case of Feliformia as a whole. On the other hand, the existence of relationships between variables identified by Mantel Tests, but not by PGLS/D-PGLS (and vice-versa) brings attention to one important point: neither Mantel Tests nor PGLS/D-PGLS may be considered as a "golden standard" for Phylogenetic Comparative Analyses of Phenotypic Integration. For Mantel Tests, this results both from the previously mentioned generally low power and also from differences in meaning between a variable and "pairwise distances between variables", which is the raw material on which Mantel Tests operate (Dutilleul *et al*, 2000), which may complicate the interpretation of the value of correlations between variables. The use of PGLS/D-PGLS for analyses of integration likewise suffer from at least two problems. Firstly, since Integration Patterns (as well as other variables, like Diet and Sociality here) are primarily represented as similarities (e.g. Random Skewers - Cheverud & Marroig, 2001), some sort of method must be used to convert them into variables in order to use these methods. The solution employed here for this problem was the use of a Principal Coordinate Analysis (PCO - Gower, 1966). After computing a PCO, however, one further decision must be taken regarding the number of axes to include in the Comparative Analysis. Here we decided to use all axes with positive eigenvalues, a method which aims at keeping the highest possible amount of the variation included in the original similarity matrix, but may be sub-optimal in some cases (Tsang & Pereira, 2014). Alternative choices regarding the number of axes to use in the analyses based on different principles are possible, and it is uncertain to what degree they may affect the results obtained. Secondly, the recently proposed D-PGLS analyses (Adams, 2014b)'s limitation of not allowing simultaneous estimation of the Phylogenetic Signal to be embedded in the model's error structure makes it uncertain whether a phylogenetic regression model should be preferred to a non-phylogenetic model in some cases. This is particularly the case when a significant relationship between variables is identified only with a non-phylogenetic model (or only with a phylogenetic one). The comparison of results with MANOVAs based on

phylogenetic groups as done here and in Adams (2014b) may help interpret the results, but does not seem to clear results as satisfactorily as a simultaneous estimation of Phylogenetic Signal as done with PGLS_λ (Freckleton *et al* 2002; Revell, 2010) would. Finally, the use of models based on Brownian Motion for analysing the evolution of a variational property such as Integration is itself does not yet seem to be clearly justified on theoretical grounds, even though this has been done by other authors in the past (Haber, 2015a; Linde-Medina *et al*, 2016).

Conclusion

All in all, the short assessment of alternative Phylogenetic Comparative methods and tests for Phylogenetic Signal performed here show a general agreement of Mantel Tests and alternative methods (K/Kmult, PGLS/D-PGLS), which at the same time lends support to continued use of Mantel Tests (using Phylogenetic Regressions for Comparative Methods as suggested by Harmon & Glor, 2010) and seems to provide at least some support to the use of methods based on evolutionary models for the analysis of Integration, since PGLS results for r^2 and D-PGLS results for Integration Patterns agree in most cases to those of Mantel Tests. The existence of some differences between methods and the theoretical doubts still involved in the use of both methods, however, stress the importance of further methodological analyses of Phylogenetic methods in Integration, using both empirical and simulated data and possibly including other recent methods for the assessment of Phylogenetic structure in covariance matrix evolution like those proposed by Pavoine *et al* (2010) and Jombart *et al* (2010) employed to analyse the evolution of phenotypic integration in Haber (2015b).

References

- Adams, D.C. 2014a. A Generalized K Statistic for Estimating Phylogenetic Signal from Shape and Other High-Dimensional Multivariate Data. *Systematic Biology* 63(5): 685-697.
- Adams, D.C. 2014b. A method for assessing phylogenetic least squares models for shape and other high-dimensional multivariate data. *Evolution* 68(9): 2675-2688.
- Anderson, T.W. 2003. An introduction to multivariate statistical analysis (3rd ed.). New York: John Wiley & Sons.
- Blomberg, S.P.; Garland, T.; Ives, A.R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57: 717-745.
- Dutilleul, P.; Stockwell, J.D.; Frigon, D.; Legendre, P. 2000. The Mantel Test versus Pearson's correlation analysis: assessment of the differences for biological and environmental studies. *Journal of Agricultural, Biological and Environmental Statistics* 5(2): 131-150.
- Fisher, R.A. 1924. The influence of rainfall on the yield of wheat at Rothamsted. *Philosophical Transactions of the Royal Society of London. Series B* 213: 89-142. Available at <http://links.jstor.org/sici?sici=0264-3960%281925%29213%3C89%3ATIOROT%3E2.0.CO%3B2-F>.

- Freckleton, R.P.; Harvey, P.H.; Pagel, M. 2002. Phylogenetic Analysis and Comparative Data: A Test and Review of Evidence. *The American Naturalist* 160(6): 712-726.
- Goswami, A. 2006. Morphological integration in the carnivorous skull. *Evolution* 60 (1): 169-183.
- Gower, J.C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* 53(3/4):325-338.
- Gower, J.C.; Legendre, P. 1986. Metric and Euclidean properties of dissimilarity coefficients. *Journal of classification* 3(1): 5-48.
- Grafen, A. 1989. The Phylogenetic Regression. *Philosophical Transactions of the Royal Society B: Biological Sciences* 326 (1233): 119-157. doi: 10.1098/rstb.1989.0106
- Guillot, G.; Rousset, F. 2013. Dismantling the Mantel tests. *Methods in Ecology and Evolution* 2013 (4): 336-344.
- Haber, A. 2015a. Phenotypic Covariation and Morphological Diversification In The Ruminant Skull. bioRxiv: 017553
- Haber, A. 2015b. Evolution of Morphological Integration in the Ruminant Skull. *Evolutionary Biology* 42: 99-114.
- Harmon, L.J.; Glor, R.E. 2010. Poor Statistical Performance of the Mantel Test in Phylogenetic Comparative Analyses. *Evolution* 64(7): 2173-2178.
- Jombart, T.; Pavoine, S.; Devillard, S.; Pontier, D. 2010. Putting phylogeny into the analysis of biological traits: A methodological approach. *Journal of Theoretical Biology* 264(3): 693-701.
- Lapointe, F.J.; Garland, T. 2001. A generalized permutation model for the analysis of cross-species data. *Journal of Classification* 18: 109-127.
- Lapointe, F.J.; Legendre, P. 1995. Comparison tests for dendrograms: a comparative evaluation. *Journal of Classification* 12: 265-282.
- Legendre, P. 2000. Comparison of permutation methods for the partial correlation and partial mantel tests. *Journal of Statistical Computation and Simulation* 67(1): 37-73
- Linde-Medina, M.; Boughner, J.C.; Santana, S.E.; Diogo, R. 2016. Are more diverse parts of the mammalian skull more labile? *Ecology and Evolution* 6(8): 2318-2324.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27(2): 209-220.
- Marroig, G.; Cheverud J.M.. 2001. A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology, and ontogeny during cranial evolution of new world monkeys. *Evolution* 55(12): 2576-600.
- Martins, E.P.; Hansen, T.F. 1997. Phylogenies and the Comparative Method: A General Approach to Incorporating Phylogenetic Information into the analysis of Interspecific Data. *The American Naturalist* 149 (4): 646. doi: 10.1086/286013.
- Oden, N.L.; Sokal, R.R. 1992. An Investigation of Three-Matrix Permutation Tests. *Journal of Classification* 9: 275-290.
- Oksanen, J.; Blanchet, F.G.; Kindt, R.; Legendre, P.; Minchin, P.R.; O'Hara, R.B.; Simpson, G.L.; Solymos, P.; Henry, M.; Stevens, H.; Wagner, H. 2015. *vegan: Community Ecology Package*. R package version 2.3-2. <<https://CRAN.R-project.org/package=vegan>>
- Oliveira, F.B.; Porto, A.; Marroig, G. 2009. Covariance structure in the skull of Catarrhini: a case of pattern stasis and magnitude evolution. *Journal of Human Evolution* 56(4): 417-430.
- Orme, D.; Freckleton, R.; Thomas, G.; Petzoldt, T.; Fritz, S.; Isaac, N.; Pearse, W. 2013. *caper: Comparative Analyses of Phylogenetics and Evolution in R*. R package version 0.5.2. <<https://CRAN.R-project.org/package=caper>>
- Pagel, M. 1999. Inferring the historical pattern of biological evolution. *Nature* 401: 877-884.
- Pavoine, S.; Baguette, M.; Bonsall, M.B. 2010. Decomposition of trait diversity among the nodes of a phylogenetic tree. *Ecological Monographs* 80(3): 485-507.
- Porto, A.; Oliveira, F.B.; Shirai, L.T.; de Conto, V.; Marroig, G. 2009. The Evolution of Modularity in the Mammalian Skull I: Morphological Integration Patterns and Magnitudes. *Evolutionary Biology* 36:118-135.
- Revell, L.J. 2010. Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution* 1: 319-329.
- Revell, L.J. 2012. *phytools: An R package for phylogenetic comparative biology (and other things)*. *Methods in Ecology and Evolution* 3: 217-223. doi: 10.1111/j.2041-210X.2011.00169.x
- Smouse, P.E.; Long, J.C.; Sokal, R.R. 1986. Multiple Regression and Correlation Extensions of the Mantel Test of Matrix Correspondence. *Systematic Zoology* 35(4): 627-632
- Tsang, J.; Pereira, R. 2014. Taking all positive eigenvectors is suboptimal in classical multidimensional scaling. *arXiv preprint* 1402.2703.

van Valen, L.M. 1974. Multivariate structural statistics in natural history. *Journal of Theoretical Biology* 45: 235-247.

Appendix 17 - Proportion of significant results for SRD for comparisons between and within different Feliformia taxonomic groups.

Table A17-1 - Proportion of significant results by character for Selection Response Decomposition (SRD) tests on the 53 Feliform taxa with better-estimated matrices, for comparisons at different taxonomic levels. Characters PT-TSP to BA-OPI shown in the next page. # comp = # comparisons.

add	# comp	IS-PM	IS-NLE	IS-PNS	PM-ZS	PM-ZI	PM-MT	NLE-NON	NLE-ZS	NLE-ZI	NON-BR	NON-PNS	BR-PT	BR-APET	PT-APET	PT-BA	PT-EAM	PT-ZYGI
Total	1378	0.148	0.006	0.000	0.004	0.032	0.000	0.372	0.035	0.012	0.176	0.040	0.655	0.072	0.185	0.001	0.068	0.007
Within Families																		
Felidae	231	0.000	0.000	0.000	0.000	0.004	0.000	0.225	0.078	0.000	0.017	0.000	0.489	0.009	0.338	0.000	0.004	0.000
Eupleridae	10	0.000	0.000	0.000	0.000	0.000	0.000	0.400	0.000	0.000	0.200	0.000	0.100	0.000	0.000	0.000	0.000	0.000
Viverridae	55	0.291	0.000	0.000	0.000	0.018	0.000	0.309	0.000	0.036	0.145	0.164	0.855	0.182	0.000	0.000	0.055	0.036
Herpestidae	36	0.250	0.056	0.000	0.000	0.000	0.000	0.278	0.000	0.000	0.000	0.000	0.694	0.000	0.056	0.000	0.083	0.000
Hyaenidae	6	0.333	0.000	0.000	0.000	0.000	0.000	0.667	0.000	0.000	0.333	0.000	0.333	0.000	0.000	0.000	0.000	0.000
Family vs all others																		
Felidae vs others	660	0.100	0.002	0.000	0.008	0.052	0.000	0.388	0.024	0.014	0.195	0.048	0.650	0.079	0.217	0.002	0.095	0.003
Eupleridae vs others	235	0.068	0.004	0.000	0.000	0.034	0.000	0.332	0.009	0.009	0.166	0.013	0.523	0.043	0.149	0.000	0.123	0.017
Viverridae vs others	451	0.173	0.002	0.000	0.011	0.060	0.000	0.277	0.013	0.029	0.175	0.078	0.792	0.182	0.160	0.002	0.102	0.018
Herpestidae vs others	387	0.163	0.013	0.000	0.000	0.013	0.000	0.452	0.008	0.008	0.150	0.047	0.736	0.047	0.129	0.000	0.072	0.000
Hyaenidae vs others	192	0.125	0.021	0.000	0.000	0.042	0.000	0.521	0.021	0.010	0.323	0.016	0.505	0.047	0.099	0.000	0.042	0.010
Prionodontidae vs others	51	1.000	0.000	0.000	0.000	0.000	0.000	0.980	0.275	0.000	0.725	0.000	0.980	0.020	0.255	0.000	0.000	0.000
Nandiniidae vs others	51	0.059	0.000	0.000	0.000	0.039	0.000	0.275	0.020	0.020	0.216	0.020	0.725	0.020	0.098	0.000	0.000	0.000
Sister groups																		
Prionodontidae x Felidae	21	1.000	0.000	0.000	0.000	0.000	0.000	1.000	0.333	0.000	0.857	0.000	1.000	0.000	0.238	0.000	0.000	0.000
Prionodon/Felidae vs others	644	0.146	0.002	0.000	0.008	0.053	0.000	0.408	0.031	0.014	0.200	0.050	0.669	0.082	0.224	0.002	0.098	0.003
Viverridae vs Hy He Eu	187	0.198	0.005	0.000	0.000	0.027	0.000	0.294	0.000	0.027	0.139	0.064	0.781	0.160	0.053	0.000	0.086	0.027
Hyaenidae vs He Eu	52	0.192	0.058	0.000	0.000	0.000	0.000	0.365	0.000	0.000	0.231	0.000	0.500	0.019	0.135	0.000	0.058	0.000
Herpestidae vs Eupleridae	36	0.167	0.000	0.000	0.000	0.000	0.000	0.472	0.000	0.000	0.111	0.000	0.667	0.028	0.000	0.000	0.111	0.000
Other comparisons																		
Hyaenidae vs Felidae	84	0.071	0.000	0.000	0.000	0.083	0.000	0.607	0.048	0.024	0.429	0.000	0.357	0.000	0.119	0.000	0.024	0.000
Hyaenidae vs Viv + He Eu	96	0.188	0.031	0.000	0.000	0.000	0.000	0.406	0.000	0.000	0.198	0.031	0.646	0.094	0.094	0.000	0.052	0.021
Herpestidae vs Viverridae	90	0.256	0.000	0.000	0.000	0.033	0.000	0.211	0.000	0.033	0.100	0.078	0.833	0.156	0.089	0.000	0.056	0.000

Table A17-1 (cont.) Characters PT-TSP
to BA-OPI

	# comp	PT-TSP	ZS-ZI	ZI-MT	ZI-ZYGI	ZI-TSP	MT-PNS	PNS-APET	APET-BA	APET-TS	BA-EAM	EAM-ZYGI	ZYGI-TSP	LD-AS	BR-LD	OPI-LD	PT-AS	JP-AS	BA-OPI
Total	1378	0.809	0.328	0.354	0.187	0.126	0.187	0.192	0.099	0.659	0.044	0.309	0.039	0.534	0.499	0.496	0.229	0.656	0.876
Within Families																			
Felidae	231	0.887	0.143	0.390	0.000	0.000	0.035	0.022	0.000	0.541	0.000	0.065	0.000	0.420	0.645	0.221	0.082	0.584	0.918
Eupleridae	10	0.400	0.500	0.700	0.200	0.300	0.100	0.200	0.400	0.800	0.000	0.000	0.400	0.300	0.400	0.400	0.500	1.000	0.900
Viverridae	55	0.673	0.182	0.291	0.182	0.073	0.364	0.073	0.018	0.964	0.000	0.309	0.000	0.909	0.327	0.855	0.109	0.745	0.782
Herpestidae	36	0.944	0.472	0.222	0.417	0.250	0.194	0.222	0.000	0.417	0.000	0.583	0.000	0.500	0.361	0.472	0.361	0.889	0.944
Hyaenidae	6	0.833	0.500	0.500	0.167	0.333	0.333	0.667	0.667	0.500	0.500	0.833	0.000	0.500	0.500	0.667	0.167	0.167	0.833
Family vs all others																			
Felidae vs others	660	0.820	0.385	0.338	0.165	0.100	0.194	0.159	0.092	0.618	0.056	0.289	0.029	0.512	0.542	0.458	0.262	0.642	0.862
Eupleridae vs others	235	0.681	0.430	0.502	0.094	0.055	0.140	0.345	0.213	0.719	0.026	0.123	0.196	0.379	0.536	0.438	0.345	0.885	0.872
Viverridae vs others	451	0.838	0.302	0.304	0.151	0.102	0.271	0.082	0.073	0.807	0.016	0.288	0.031	0.643	0.477	0.690	0.239	0.661	0.803
Herpestidae vs others	387	0.842	0.403	0.251	0.240	0.204	0.271	0.204	0.062	0.581	0.026	0.463	0.023	0.504	0.460	0.481	0.331	0.765	0.930
Hyaenidae vs others	192	0.797	0.443	0.490	0.391	0.063	0.203	0.380	0.443	0.578	0.271	0.526	0.031	0.495	0.448	0.573	0.219	0.495	0.870
Prionodontidae vs others	51	0.569	0.176	0.353	0.824	0.882	0.020	1.000	0.000	1.000	0.000	0.922	0.039	0.941	0.039	0.902	0.039	0.157	1.000
Nandiniidae vs others	51	0.863	0.353	0.451	0.098	0.078	0.216	0.098	0.059	0.529	0.039	0.196	0.039	0.490	0.647	0.314	0.157	0.647	0.804
Sister groups																			
Prionodontidae x Felidae	21	0.667	0.238	0.190	0.905	0.905	0.000	1.000	0.000	1.000	0.000	0.905	0.000	1.000	0.095	0.952	0.000	0.048	1.000
Prionodon/Felidae vs others	644	0.793	0.390	0.323	0.177	0.140	0.200	0.205	0.095	0.657	0.057	0.335	0.033	0.516	0.512	0.477	0.241	0.644	0.862
Viverridae vs Hy He Eu	187	0.807	0.289	0.305	0.203	0.123	0.321	0.187	0.155	0.829	0.037	0.390	0.075	0.626	0.396	0.749	0.278	0.791	0.845
Hyaenidae vs He Eu	52	0.827	0.538	0.500	0.288	0.135	0.173	0.442	0.481	0.596	0.173	0.577	0.096	0.365	0.385	0.538	0.231	0.731	0.923
Herpestidae vs Eupleridae	36	0.667	0.472	0.528	0.222	0.111	0.139	0.556	0.222	0.778	0.028	0.250	0.222	0.333	0.500	0.417	0.444	0.889	0.944
Other comparisons																			
Hyaenidae vs Felidae	84	0.786	0.500	0.512	0.500	0.024	0.167	0.405	0.440	0.488	0.369	0.464	0.000	0.476	0.512	0.500	0.214	0.321	0.869
Hyaenidae vs Viv + He Eu	96	0.823	0.396	0.479	0.281	0.104	0.240	0.354	0.438	0.677	0.167	0.583	0.063	0.521	0.354	0.656	0.219	0.635	0.885
Herpestidae vs Viverridae	90	0.867	0.300	0.211	0.256	0.189	0.367	0.167	0.011	0.778	0.000	0.444	0.011	0.633	0.311	0.800	0.311	0.811	0.900

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Table A18-2. Raw (below diagonal) and Adjusted (above diagonal) RS similarity for all pairwise comparisons between the 53 better-estimated matrices.

Taxon codes: Na (Nandiniidae) - Nand (Nandiniinae) - 1: *Nandinia binotata*.

Hy (Hyaenidae) - Prot (Protelinae) - 2: *Proteles cristata*;

Hyae (Hyaeninae) - 3: *Hyaena hyaena*, 4: *Parahyaena brunnea*, 5: *Crocota crocuta*.

Eu (Eupleridae) - Mong (Galidiinae - malagasy mongooses) - 6: *Salanoia concolor*, 7: *Galidia elegans*

Civ (Euplerinae - malagasy civets) - 8: *Fossa fossana*, 9: *Eupleres goudotii*

Cry (Cryptoproctinae) - 10: *Cryptoprocta* (Genus)

He (Herpestidae) - Soc (Mungotinae - Social mongooses) - 11: *Suricata suricatta*, 12: *Mungos mungo*, 13: *Helogale parvula*, 14: *Crossarchus* (Genus)

Non (Herpestinae - Non-social mongooses) - 15: *Urva javanica*, 16: *Urva urva*, 17: *Galerella sanguinea* group, 18: *Cynictis penicillata*, 19: *Atilax paludinosus*

Vi (Viverridae) - Gen (Genettinae) - 20: *Genetta servalina*, 21: *Genetta genetta*, 22: *Genetta maculata*

Viv (Viverrinae) - 23: *Viverricula indica*, 24: *Viverra zibetha*, 25: *Civettictis civetta*

Par (Paradoxurinae + Hemigalinae) - 26: *Arctogalidia* (Genus), 27: *Hemigalus derbyanus*, 28: *Paguma larvata*, 29: *Paradoxurus musanga*, 30: *Arctictis binturong*

Pr (Prionodontidae) - Prio (Prionodontinae) - 31: *Prionodon* (Genus)

Fel (Felidae) - Pant (Pantherinae) - 32: *Panthera uncia*, 33: *Panthera tigris*, 34: *Panthera onca*, 35: *Panthera pardus*, 36: *Panthera leo*, 37: *Neofelis* (Genus)

Fel (Felinae) - 38: *Leptailurus serval*, 39: *Caracal caracal*, 40: *Catopuma temminckii*, 41: *Leopardus wiedii*, 42: *Leopardus mitis*, 43: *Leopardus tigrinus* group, 44: *Leopardus geoffroyi*, 45: *Prionailurus bengalensis*, 46: *Felis margarita*, 47: *Felis*

catus, 48: *Felis silvestris*, 49: *Lynx rufus*, 50: *Lynx lynx*, 51: *Puma yagouaroundi*, 52: *Puma concolor*, 53: *Acinonyx jubatus*

		Na	Hy					Eu					He					V1					Pr	Fe																															
		Nand	Prot	Hyae			Mong		Civ			Cry	Soc				Non					Gen			Viv		Par			Prio	Pant					Fel																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	
Na	Nand	1	0.95	0.82	0.80	0.70	0.78	0.80	0.86	0.84	0.70	0.91	0.72	0.90	0.86	0.77	0.76	0.83	0.83	0.85	0.83	0.76	0.84	0.91	0.85	0.80	0.86	0.81	0.76	0.83	0.94	0.79	0.59	0.80	0.80	0.86	0.82	0.86	0.87	0.87	0.90	0.86	0.82	0.89	0.80	0.88	0.90	0.85	0.84	0.86	0.85	0.87	0.84	0.83	0.82
Hy	Prot	2	0.77	0.92	0.80	0.76	0.81	0.77	0.83	0.85	0.76	0.74	0.77	0.87	0.86	0.85	0.77	0.83	0.84	0.87	0.87	0.78	0.84	0.89	0.85	0.80	0.83	0.82	0.80	0.78	0.77	0.79	0.67	0.71	0.72	0.79	0.73	0.71	0.75	0.76	0.81	0.81	0.77	0.79	0.77	0.74	0.77	0.72	0.78	0.78	0.77	0.73	0.77	0.78	0.74
	Hyae	3	0.75	0.74	0.93	0.86	0.90	0.81	0.82	0.80	0.73	0.71	0.73	0.85	0.82	0.80	0.70	0.76	0.78	0.80	0.79	0.69	0.76	0.81	0.73	0.74	0.81	0.77	0.75	0.72	0.73	0.78	0.56	0.81	0.67	0.81	0.74	0.72	0.74	0.78	0.83	0.80	0.79	0.82	0.77	0.76	0.78	0.75	0.81	0.74	0.76	0.74	0.78	0.82	0.84
		4	0.66	0.70	0.80	0.93	0.85	0.73	0.75	0.71	0.64	0.65	0.74	0.77	0.77	0.74	0.65	0.69	0.69	0.76	0.73	0.64	0.73	0.76	0.73	0.75	0.76	0.72	0.69	0.64	0.69	0.75	0.53	0.73	0.62	0.72	0.68	0.63	0.65	0.69	0.74	0.75	0.73	0.79	0.70	0.66	0.66	0.66	0.70	0.68	0.71	0.68	0.71	0.71	0.77
		5	0.73	0.75	0.84	0.79	0.93	0.75	0.80	0.81	0.64	0.67	0.79	0.83	0.84	0.80	0.72	0.74	0.82	0.82	0.79	0.70	0.77	0.81	0.75	0.77	0.82	0.74	0.75	0.73	0.68	0.79	0.59	0.75	0.69	0.81	0.74	0.74	0.74	0.72	0.77	0.78	0.77	0.76	0.83	0.79	0.75	0.73	0.73	0.77	0.76	0.74	0.74	0.78	0.78
Eu	Mong	6	0.73	0.70	0.73	0.66	0.68	0.88	0.84	0.80	0.68	0.76	0.67	0.89	0.78	0.74	0.77	0.83	0.79	0.81	0.80	0.73	0.71	0.84	0.76	0.75	0.79	0.76	0.69	0.71	0.77	0.84	0.51	0.72	0.62	0.74	0.71	0.66	0.72	0.68	0.79	0.75	0.69	0.78	0.74	0.75	0.77	0.70	0.75	0.72	0.68	0.69	0.73	0.80	0.73
	Civ	7	0.81	0.78	0.76	0.70	0.75	0.77	0.94	0.83	0.70	0.81	0.76	0.88	0.90	0.82	0.78	0.83	0.84	0.84	0.88	0.76	0.87	0.87	0.81	0.83	0.85	0.82	0.76	0.81	0.84	0.83	0.61	0.82	0.77	0.79	0.78	0.77	0.81	0.81	0.85	0.82	0.81	0.87	0.78	0.84	0.82	0.82	0.83	0.83	0.81	0.81	0.80	0.82	0.83
		8	0.78	0.78	0.74	0.66	0.75	0.72	0.77	0.91	0.70	0.80	0.74	0.88	0.85	0.75	0.81	0.80	0.78	0.89	0.84	0.79	0.82	0.87	0.83	0.80	0.86	0.79	0.70	0.79	0.81	0.75	0.54	0.71	0.74	0.84	0.82	0.78	0.82	0.76	0.79	0.79	0.70	0.81	0.72	0.81	0.79	0.74	0.76	0.79	0.77	0.75	0.75	0.85	0.77
		9	0.63	0.67	0.64	0.57	0.57	0.59	0.62	0.61	0.84	0.65	0.69	0.75	0.69	0.76	0.69	0.66	0.71	0.72	0.71	0.65	0.75	0.72	0.68	0.70	0.67	0.70	0.71	0.69	0.71	0.63	0.60	0.65	0.55	0.57	0.62	0.54	0.62	0.62	0.70	0.66	0.64	0.67	0.66	0.66	0.64	0.67	0.66	0.66	0.63	0.59	0.68		
Cry	10	0.86	0.69	0.67	0.62	0.64	0.69	0.77	0.75	0.58	0.96	0.67	0.86	0.77	0.68	0.73	0.75	0.79	0.81	0.74	0.69	0.81	0.87	0.80	0.75	0.79	0.71	0.67	0.76	0.92	0.73	0.54	0.74	0.77	0.81	0.79	0.86	0.85	0.81	0.88	0.88	0.75	0.83	0.72	0.85	0.86	0.79	0.83	0.83	0.78	0.85	0.81	0.76	0.79	
He	Soc	11	0.68	0.72	0.68	0.69	0.73	0.61	0.71	0.69	0.61	0.63	0.93	0.78	0.75	0.81	0.70	0.67	0.75	0.75	0.77	0.67	0.80	0.73	0.73	0.79	0.79	0.77	0.73	0.72	0.69	0.68	0.58	0.68	0.66	0.67	0.66	0.63	0.64	0.68	0.69	0.71	0.67	0.74	0.70	0.69	0.64	0.64	0.75	0.74	0.69	0.66	0.69	0.69	0.76
		12	0.86	0.82	0.80	0.73	0.78	0.82	0.84	0.82	0.67	0.82	0.74	0.96	0.87	0.82	0.79	0.85	0.88	0.91	0.87	0.77	0.85	0.91	0.84	0.84	0.89	0.82	0.76	0.83	0.85	0.82	0.60	0.81	0.78	0.83	0.82	0.81	0.83	0.82	0.88	0.88	0.79	0.89	0.80	0.87	0.87	0.81	0.85	0.84	0.81	0.82	0.83	0.82	0.83
		13	0.81	0.80	0.77	0.72	0.79	0.70	0.84	0.78	0.61	0.73	0.70	0.82	0.93	0.81	0.81	0.85	0.86	0.88	0.88	0.81	0.83	0.87	0.86	0.81	0.84	0.82	0.76	0.79	0.80	0.84	0.66	0.77	0.76	0.80	0.72	0.75	0.78	0.82	0.84	0.81	0.84	0.85	0.85	0.82	0.79	0.79	0.78	0.81	0.80	0.77	0.82	0.82	0.79
		14	0.73	0.79	0.75	0.69	0.75	0.67	0.77	0.70	0.68	0.64	0.76	0.78	0.76	0.94	0.78	0.78	0.79	0.77	0.88	0.75	0.86	0.82	0.81	0.84	0.84	0.80	0.88	0.80	0.75	0.74	0.66	0.77	0.76	0.62	0.69	0.63	0.64	0.70	0.74	0.66	0.68	0.68	0.75	0.72	0.73	0.69	0.71	0.73	0.72				
	Non	15	0.72	0.72	0.65	0.61	0.68	0.70	0.73	0.75	0.61	0.69	0.66	0.75	0.76	0.73	0.94	0.81	0.82	0.81	0.85	0.76	0.77	0.82	0.82	0.78	0.80	0.82	0.67	0.78	0.75	0.77	0.64	0.69	0.67	0.75	0.70	0.64	0.73	0.71	0.73	0.77	0.73	0.76	0.73	0.66	0.69	0.75	0.68	0.68	0.67	0.75	0.70		
		16	0.78	0.77	0.71	0.65	0.69	0.75	0.78	0.73	0.59	0.70	0.63	0.80	0.80	0.73	0.75	0.93	0.83	0.86	0.89	0.74	0.79	0.88	0.85	0.85	0.81	0.82	0.68	0.84	0.79	0.82	0.58	0.73	0.72	0.77	0.72	0.71	0.75	0.75	0.78	0.77	0.79	0.79	0.80	0.81	0.78	0.72	0.76	0.78	0.76				
		17	0.79	0.78	0.73	0.65	0.77	0.72	0.79	0.72	0.64	0.75	0.70	0.84	0.81	0.74	0.77	0.78	0.94	0.82	0.84	0.77	0.80	0.85	0.80	0.78	0.83	0.80	0.71	0.81	0.83	0.81	0.66	0.72	0.72	0.77	0.76	0.74	0.77	0.81	0.85	0.84	0.79	0.84	0.84	0.85	0.83	0.78	0.84	0.83	0.76	0.76	0.81	0.76	0.80
		18	0.81	0.81	0.75	0.71	0.77	0.74	0.79	0.83	0.64	0.77	0.70	0.87	0.82	0.73	0.77	0.80	0.77	0.94	0.87	0.80	0.83	0.89	0.86	0.81	0.84	0.84	0.69	0.77	0.82	0.79	0.61	0.74	0.71	0.78	0.76	0.75	0.78	0.77	0.77	0.80	0.72	0.81	0.75	0.79	0.77	0.74	0.77	0.80	0.78	0.75	0.75	0.81	0.76
		19	0.78	0.81	0.74	0.68	0.74	0.72	0.83	0.77	0.63	0.70	0.72	0.82	0.82	0.82	0.80	0.82	0.78	0.81	0.93	0.76	0.86	0.89	0.87	0.87	0.89	0.89	0.79	0.85	0.83	0.83	0.59	0.81	0.70	0.78	0.76	0.73	0.75	0.77	0.79	0.79	0.79	0.80	0.77	0.73	0.77	0.79	0.80	0.75	0.75	0.83	0.76	0.79	
Gen	20	0.72	0.73	0.64	0.60	0.66	0.66	0.71	0.73	0.58	0.65	0.63	0.73	0.76	0.70	0.71	0.69	0.72	0.75	0.71	0.93	0.81	0.81	0.83	0.77	0.78	0.74	0.74	0.76	0.73	0.69	0.72	0.65	0.66	0.74	0.68	0.65	0.69	0.67	0.74	0.74	0.74	0.80	0.70	0.68	0.65	0.70	0.69	0.69	0.73	0.77	0.65			
	21	0.79	0.78	0.71	0.68	0.72	0.64	0.81	0.75	0.66	0.77	0.75	0.81	0.78	0.81	0.72	0.74	0.75	0.78	0.78	0.76	0.94	0.89	0.89	0.88	0.87	0.83	0.81	0.86	0.83	0.75	0.66	0.75	0.73	0.76	0.77	0.75	0.75	0.76	0.78	0.83	0.81	0.81	0.79	0.78	0.76	0.77	0.82	0.79	0.81	0.79	0.79	0.78		
	22	0.86	0.83	0.76	0.71	0.77	0.77	0.82	0.81	0.65	0.83	0.69	0.87	0.82	0.78	0.77	0.83	0.80	0.84	0.84	0.76	0.84	0.95	0.90	0.88	0.88	0.83	0.78	0.86	0.85	0.83	0.65	0.80	0.75	0.84	0.80	0.79	0.83	0.81	0.84	0.86	0.80	0.82	0.77	0.85	0.86	0.79	0.81	0.80	0.79	0.79	0.82	0.84	0.79	
Vi	Viv	23	0.81	0.80	0.69	0.68	0.70	0.70	0.77	0.77	0.61	0.76	0.68	0.80	0.81	0.77	0.77	0.80	0.75	0.81	0.82	0.78	0.83	0.86	0.94	0.83	0.85	0.81	0.78	0.84	0.83	0.76	0.67	0.68	0.68	0.79	0.71	0.70	0.74	0.74	0.72	0.79	0.83	0.76	0.78	0.79	0.76	0.76	0.69	0.74	0.76	0.77	0.76	0.77</	

Appendix 19 - Specimens reidentified during data collection and data analysis

Table A19-1 - Specimens reidentified during data collection and data analysis. AMNH = American Museum of Natural History (Nova Iorque); MNHN = Muséum National d'Histoire Naturelle (Paris); MNRJ = Museu Nacional da Universidade Federal do Rio de Janeiro; MZUSP = Museu de Zoologia da Universidade de São Paulo; NMP = Národní muzeum (Praga); NMW = Naturhistorisches Museum Wien (Viena); Naturalis = Naturalis Biodiversity Centre (Leiden); UMZC = University Museum of Zoology, Cambridge; SMF = Naturmuseum Senckenberg (Frankfurt am Main); ZMB-MAM = Museum für Naturkunde, Berlin. ZFMK = Zoologisches Forschungsmuseum Alexander Koenig (Bonn).

ID	Original species	New species	Change	Phase	Obs	Confirmation/Source
AMNH 103341	<i>Paradoxurus lignicolor</i>	<i>Paradoxurus philippinensis</i>	yes	Data collection, data analysis	done	Veron et al 2014
AMNH 133977	<i>Leopardus braccatus</i>	<i>Leopardus colocolo braccatus</i>	yes	Data analysis (but not directly)	done - braccatus, pajeros and colocolo seem to be all within colocolo (Eizirik et al, in prep)	Eizirik et al, in prep; Garcia Perea 1994
AMNH 16695	<i>Leopardus pajeros</i>	<i>Leopardus colocolo pajeros</i>	yes	Data analysis	done - braccatus, pajeros and colocolo seem to be all within colocolo (Eizirik et al, in prep)	Eizirik et al, in prep
AMNH 169443	<i>Galerella sanguinea</i>	<i>Galerella sanguinea south</i>	no	Data analysis	done	Kept as southern sanguinea (" <i>Galerella sanguinea south</i> "), possibly separate species from " <i>Galerella sanguinea central</i> " from Central/East Africa (Rapson et al 2012). Only individual this large from area though! Checking others and more <i>pulverulenta</i> in the future. might be interesting.
AMNH 19383	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
AMNH 22916	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
AMNH 243110	<i>Leopardus colocolo budini?</i>	<i>Leopardus colocolo munoai</i>	yes	Data analysis (but not directly)	done - braccatus, pajeros and colocolo seem to be all within colocolo (Eizirik et al, in prep)	Eizirik et al, in prep; Garcia Perea 1994
AMNH 35273	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
AMNH 35808	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
AMNH 64448	<i>Parahyaena brunnea</i>	<i>Hyaena hyaena</i>	yes	Data analysis	done	LDA groups clearly with <i>Hyaena hyaena</i>
AMNH 76150	<i>Leopardus colocolo thomasi?</i>	<i>Leopardus colocolo garleppi</i>	yes	Data analysis (but not directly)	done - garleppi seems to be ssp of 'braccatus' branch; braccatus, pajeros and colocolo seem to be all within "colocolo" (Eizirik et al, in prep)	Garcia Perea 1994; Napolitano et al 2008
AMNH 81834	<i>Crocota crocuta</i>	<i>Parahyaena brunnea</i>	yes	Data collection	done	Character clear (Rieger, 1981; Mills, 1982); other researcher had already indicated so in museum.
MNHN 1393-192	<i>Crossarchus platycephalus</i>	<i>Mungos mungo</i>	yes	Data analysis	done	LDA

ID	Original species	New species	Change	Phase	Obs	Confirmation/Source
MNHN 1902-530	<i>Crossarchus ansorgei</i>	<i>Mungos mungo</i>	yes	Data analysis	done	LDA
MNHN 1909-437	<i>Leopardus jacobitus</i>	<i>Leopardus colocolo</i>	yes	Data analysis	done - braccatus, pajeros and colocolo seem to be all within colocolo (Eizirik et al, in prep)	Eizirik et al, in prep, Napolitano et al 2008; Garcia-Perea, 1994; Garcia-Perea, 2002.
MNHN 1974-321	<i>Galerella sanguinea</i>	<i>Galerella sanguinea</i>	no	Data analysis	done	Seems slightly different from central <i>sanguinea</i> PC, but still far from type of <i>erlangeri</i> ("ochracea" sample here). LDA shows grouping with central <i>sanguinea</i> . Kept as central <i>sanguinea</i> (<i>Galerella sanguinea</i> from Central/East africa, possibly separate species from <i>Galerella sanguinea</i> from South Africa - Rapson et al 2012)
MNHN 1979-52	<i>Panthera uncia</i>	<i>Panthera onca</i>	yes	Data analysis	done	LDA groups with <i>onca</i>
MNHN A-3457	<i>Leopardus pajeros</i>	<i>Leopardus geoffroyi</i>	yes	Data analysis	done	Garcia Perea 1994; Nascimento 2014
MNRJ 0	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MNRJ 0-5145	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus tigrinus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MNRJ 0-B	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MNRJ 0-C	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MNRJ 24894	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus tigrinus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MNRJ 24896	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus tigrinus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MNRJ 24911	<i>Leopardus braccatus</i>	<i>Leopardus colocolo munoai</i>	yes	Data analysis	done - braccatus, pajeros and colocolo seem to be all within colocolo (Eizirik et al, in prep)	Eizirik et al, in prep; Garcia Perea 1994
MNRJ 25650	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MNRJ 25651	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MNRJ 25726	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MNRJ 3133	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MNRJ 49354	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus tigrinus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MNRJ 49356	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MNRJ 5885	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MNRJ 610	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MNRJ 7261	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MNRJ 74386	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MNRJ 79465	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MZUSP 1168	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013

ID	Original species	New species	Change	Phase	Obs	Confirmation/Source
MZUSP 11819	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MZUSP 13602	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MZUSP 13671	<i>Leopardus braccatus</i>	<i>Leopardus colocolo</i> <i>braccatus</i>	yes	Data analysis	done - braccatus, pajeros and colocolo seem to be all within colocolo (Eizirik et al, in prep)	Eizirik et al, in prep
MZUSP 13796	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 1393	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 1395	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 1765	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 1878	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 19900	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus tigrinus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MZUSP 21613	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus tigrinus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MZUSP 22415	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MZUSP 22416	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MZUSP 22417	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MZUSP 2320	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 2321	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 2362	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 2646	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus tigrinus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 2810	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 2971	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 32283	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus tigrinus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MZUSP 32633	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 3799	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 3811	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 396	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MZUSP 401	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 6262	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 6459	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 6549	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP 6728	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013

ID	Original species	New species	Change	Phase	Obs	Confirmation/Source
MZUSP 7786	<i>Leopardus braccatus</i>	<i>Leopardus colocolo braccatus</i>	yes	Data analysis	done - braccatus, pajeros and colocolo seem to be all within colocolo (Eizirik et al, in prep)	Eizirik et al, in prep
MZUSP 810	<i>Leopardus tigrinus or guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
MZUSP TX040001	<i>Leopardus tigrinus or guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
MZUSP TX040006	<i>Leopardus braccatus</i>	<i>Leopardus colocolo braccatus</i>	yes	Data analysis	done - braccatus, pajeros and colocolo seem to be all within colocolo (Eizirik et al, in prep)	Eizirik et al, in prep
MZUSP TX050631	<i>Leopardus braccatus</i>	<i>Leopardus colocolo braccatus</i>	yes	Data analysis	done - braccatus, pajeros and colocolo seem to be all within colocolo (Eizirik et al, in prep)	Eizirik et al, in prep
MZUSP TX050665	<i>Leopardus tigrinus or guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	LDA - separation based on Trigo et al 2013
Naturalis RMNH 34770	<i>Prionodon pardicolor</i>	<i>Prionodon linsang</i>	yes	Data analysis	done	LDA groups clearly with <i>Prionodon linsang</i>
Naturalis RMNH 3478	<i>Viverra civettina</i>	<i>Hemigalus derbyanus</i>	yes	Data analysis	done - must check photo when recover access to dead HD; relatively small for <i>Hemigalus</i> . Maybe subadult or young.	Papes & Gaubert (2007) classify as <i>Viverra civettina</i> . Nandini and Mudappa (2010) - NOT <i>Viverra</i> ; PCA - far from any <i>Viverra</i> ; LDA - groups with <i>Hemigalus</i> . Still odd, maybe young. Removed from analyses.
Naturalis ZMA (?) 1975	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
NMP 46091	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
NMP 46216	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
NMP 46466	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
NMP 46703	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
NMP 46704	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
NMP 48196	<i>Felis silvestris</i>	<i>Felis silvestris ornata</i>	yes	Data analysis	done	Locality (based on Driscoll <i>et al</i> 2007)
NMP 48197	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
NMP 9782	<i>Galidictis fasciata</i>	<i>Suricata suricatta</i>	yes	Data collection	done	General appearance. Also clearly groups with <i>Suricata</i> on PCA
NMW 1176	<i>Mungos gambianus</i>	<i>Mungos mungo</i>	yes	Data analysis	done	<i>Mungos mungo</i>
NMW 1178	<i>Mungos gambianus</i>	<i>Mungos mungo</i>	yes	Data analysis	done	<i>Mungos mungo</i>
NMW 1380	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
NMW 31066	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
SMF 15719	<i>Leopardus geoffroyi</i>	<i>Leopardus mitis</i>	yes	Data analysis (but not directly)	done	Seymour 1999, Nascimento 2010
SMF 51593	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
UMZC K 5821	<i>Panthera uncia</i>	<i>Panthera pardus</i>	yes	Data analysis	done	LDA groups closer to <i>pardus</i> than <i>uncia</i> .

ID	Original species	New species	Change	Phase	Obs	Confirmation/Source
ZMB-MAM 021267_ (1) (auf Schädel steht A155.07)	<i>Galerella sanguinea</i> (Typus von "Calogale erlangeri" == " <i>Galerella sanguinea erlangeri</i> ")	<i>Galerella ochracea</i>	yes	Data collection, data analysis	done	Geometric morphometric analysis shows bulla larger, zygo wider and braincase higher than all <i>sanguinea</i> . Size smaller. PCA shows very separated from all <i>sanguinea</i> . Could not compare with other <i>ochracea</i> , but seems very likely that == <i>Galerella ochracea</i> . Taylor & Goldman (1993); Azzaroli & Simonetta (1966)
ZMB-MAM 12543	<i>Crossarchus obscurus</i>	<i>Mungos mungo</i>	yes	Data analysis	done	LDA
ZMB-MAM 12655	<i>Parahyaena brunnea</i>	<i>Hyaena hyaena</i>	yes	Data analysis	done	LDA groups with <i>Hyaena hyaena</i> ; agrees with locality in Sudan.
ZMB-MAM 14575	<i>Crossarchus obscurus</i>	<i>Crossarchus platycephalus</i>	yes	Data analysis	done	LDA
ZMB-MAM 18124	<i>Crossarchus obscurus</i>	<i>Mungos mungo</i>	yes	Data analysis	done	LDA
ZMB-MAM 19045	<i>Genetta maculata</i>	<i>Genetta servalina</i>	yes	Data analysis	done	PCA with <i>servalina</i> and <i>maculata</i> shows association with <i>servalina</i> .
ZMB-MAM 1959	<i>Viverra zibetha</i>	<i>Civettictis civetta</i>	yes	Data analysis	done	PCA shows closer to <i>Civettictis</i> ; LDA groups with <i>Civettictis</i> ; no locality information. Is relatively small for <i>Civettictis civetta</i> though!
ZMB-MAM 19677	<i>Genetta maculata</i>	<i>Genetta "letabae"</i>	yes	Data analysis	done	LDA ok. Diagnostic characters - ok
ZMB-MAM 19679	<i>Genetta maculata</i>	<i>Genetta "letabae"</i>	yes	Data analysis	done	LDA ok. Diagnostic characters - ok
ZMB-MAM 19862	<i>Genetta angolensis</i>	<i>Genetta maculata</i>	yes	Data analysis	done	PCA groups with <i>maculata</i>
ZMB-MAM 19863	<i>Genetta angolensis</i>	<i>Genetta maculata</i>	yes	Data analysis	Done	PCA groups with <i>maculata</i>
ZMB-MAM 19864	<i>Genetta angolensis</i>	<i>Genetta maculata</i>	yes	Data analysis	done	PCA groups with <i>maculata</i>
ZMB-MAM 21268	<i>Crossarchus obscurus</i>	<i>Mungos mungo</i>	yes	Data analysis	done	LDA
ZMB-MAM 21290	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
ZMB-MAM 22153	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
ZMB-MAM 2907	<i>Herpestes javanicus</i>	<i>Herpestes javanicus</i>	no	Data collection, data analysis	done	PCA shows association with <i>javanicus</i> - locality probably wrong (not Borneo)
ZMB-MAM 32405	<i>Crossarchus obscurus</i>	<i>Mungos mungo</i>	yes	Data analysis	done	LDA
ZMB-MAM 42551	<i>Crossarchus obscurus</i>	<i>Mungos mungo</i>	yes	Data analysis	done	LDA
ZMB-MAM 46451	<i>Leopardus tigrinus</i> or <i>guttulus</i>	<i>Leopardus guttulus</i>	yes	Data analysis	done	locality. Trigo et al 2013
ZMB-MAM 4929	<i>Catopuma temminckii</i>	<i>Catopuma temminckii</i>	no	Data analysis - groups with <i>temminckii</i> , not at all with <i>badia</i>	done	Kept as <i>temminckii</i> . Location must be wrong
ZMB-MAM 50748	<i>Neofelis nebulosa</i>	<i>Neofelis diardi</i>	yes	Data analysis	done	LDA
ZMB-MAM 7906	<i>Leopardus jacobitus</i>	<i>Leopardus geoffroyi</i>	yes	Data analysis (based on identification in Seymour, 1999)	done - subspecies <i>geoffroyi</i>	Seymour 1999
ZMB-MAM 82641	<i>Crossarchus obscurus</i>	<i>Crossarchus platycephalus</i>	yes	Data analysis	done	LDA

ID	Original species	New species	Change	Phase	Obs	Confirmation/Source
ZMB-MAM 82670	<i>Mungos mungo</i>	<i>Mungos gambianus</i>	yes	Data analysis	done	LDA
ZMB-MAM 82672	<i>Mungos mungo</i>	<i>Crossarchus platycephalus</i>	yes	Data analysis	done	LDA
ZMB-MAM 82780/82673 (likely 82763)	<i>Mungos mungo</i>	<i>Crossarchus platycephalus</i>	yes	Data analysis	done	LDA
ZMB-MAM 8589	<i>Crossarchus obscurus</i>	<i>Crossarchus platycephalus</i>	yes	Data analysis	done	LDA
ZMB-MAM A 2778	<i>Crossarchus obscurus</i>	<i>Mungos mungo</i>	yes	Data analysis	done	LDA
ZMB-MAM Dummy 2167	<i>Crossarchus obscurus</i>	<i>Mungos mungo</i>	yes	Data analysis	done	LDA
ZMB-MAM Dummy 2168	<i>Crossarchus obscurus</i>	<i>Mungos mungo</i>	yes	Data analysis	done	LDA
ZMB-MAM Dummy 2170? (A4298)	<i>Crossarchus obscurus</i>	<i>Mungos mungo</i>	yes	Data analysis	done	LDA
ZMB-MAM Dummy 2177?	<i>Crossarchus obscurus</i>	<i>Mungos mungo</i>	yes	Data analysis	done	LDA
ZMB-MAM Dummy 2177? (2)	<i>Crossarchus obscurus</i>	<i>Crossarchus platycephalus</i>	yes	Data analysis	done	LDA
ZMB-MAM Keine Nummer (aus dem aufgelösten Praktikumsschrank)	<i>Panthera uncia</i>	<i>Panthera pardus</i>	yes	Data analysis	done	LDA groups closer to <i>pardus</i> than <i>uncia</i> .
ZMB-MAM No number ohneangaben	<i>Crossarchus obscurus</i>	<i>Crossarchus platycephalus</i>	yes	Data analysis	done	LDA

References

- Azzaroli, L.; Simonetta, A.M. 1966. Carnivori della Somalia ex Italiana. *Monitore Zoologico Italiano*. Supplemento 1(1): 102-195.
- Driscoll, C.A.; Menotti-Raymond, M.; Roca, A.L.; Hupe, K.; Johnston, W.E.; Geffen, E.; Harley, E.H.; Delibes, M.; Pontier, D.; Kitchener, A.C.; Yamaguchi, N.; O'Brien, S.J.; Macdonald, D.W. 2007. The Near Eastern Origin of Cat Domestication. *Science* 317: 519-523.
- Eizirik, E.; Johnson, W.E.; O'Brien, S.J. in prep. Molecular systematics and revised classification of the family Felidae (Mammalia, Carnivora). *Journal of Mammalogy*. Disponível online no endereço: <http://dobzhanskycenter.bio.spbu.ru/pdf/sjop/MS636%20Eizirik%20Felid%20Taxonomy.pdf>
- Garcia-Perea, R. 1994. The Pampas Cat Group (Genus *Lynchailurus* Severtzov, 1858) (Carnivora: Felidae), a Systematic and Biogeographic Review. *American Museum Novitates* 3096(35): 1-35.
- García-Perea, R. 2002. Andean mountain cat, *Oreailurus jacobita*: Morphological description and comparison with other felines from the altiplano. *Journal of Mammalogy* 83(1): 110-124.
- Mills, M.G.L. 1982. *Hyaena brunnea*. *Mammalian Species* 194: 1-5.
- Nandini, R.; Mudappa, D. 2010. Mystery or myth: a review of history and conservation status of the Malabar Civet *Viverra civettina* Blyth, 1862. *Small Carnivore Conservation* 43: 47-59.
- Napolitano, C.; Bennett, M.; Johnson, W.E.; O'Brien, S.J.; Marquet, P.A.; Barría, I.; Poulin, E.; Iriarte, A. 2008. Ecological and biogeographical inferences on two sympatric and enigmatic Andean cat species using genetic identification of faecal samples. *Molecular ecology* 17(2): 678-690.
- Nascimento, F.O. 2010. Revisão taxonômica do gênero *Leopardus* Gray, 1842 (Carnivora, Felidae). Doctoral dissertation, Instituto de Biociências, Universidade de São Paulo.
- Nascimento, F.O. 2014. On the morphological variation and taxonomy of the Geoffroy's cat *Leopardus geoffroyi* (d'Orbigny & Gervais, 1844) (Carnivora, Felidae). *Papéis Avulsos de Zoologia* 54(11): 129-160.
- Papes, M.; Gaubert, P. 2007. Modelling ecological niches from low numbers of occurrences:

assessment of the conservation status of poorly known viverrids (Mammalia, Carnivora) across two continents. *Diversity and Distributions* 13: 890-902.

Rieger, I. 1981. *Hyaena hyaena*. *Mammalian Species* 150: 1-5.

Seymour, K.L. 1999. Taxonomy, morphology, paleontology and phylogeny of the South American small cats (Mammalia: Felidae). PhD dissertation, University of Toronto.

Taylor, M.E.; Goldman, C.A. 1993. The taxonomic status of the African mongooses,

Herpestes sanguineus, *H. nigratus*, *H. pulverulentus* and *H. ochraceus* (Carnivora: Viverridae). *Mammalia* 57(3): 375-391.

Trigo, T.C.; Schneider, A.; Oliveira, T.G.; Lehugeur, L.M.; Silveira, L.; Freitas, T.R.O.; Eizrik, E. 2013. Molecular Data Reveal Complex Hybridization and a Cryptic Species of Neotropical Wild Cat. *Current Biology* 23: 1-6.

Veron, G.; Patou, M.-L.; Tóth, M.; Goonatilake, M.; Jennings, A.P. 2014. How many species of *Paradoxurus* civets are there? New insights from India and Sri Lanka. *Journal Zool Syst and Evol Research* 53(2): 161-174.

Appendix 20 - List of subspecies used for initial classifications within each species.

Table A20.1. List of subspecies considered for initial classification based on collection localities.

Family	Species	Subspecies considered for initial classification
Eupleridae	<i>Cryptoprocta ferox</i>	NA
	<i>Cryptoprocta spelaea</i>	NA
	<i>Eupleres goudotii</i>	<i>goudotii</i> , <i>major</i>
	<i>Fossa fossana</i>	NA
	<i>Galidia elegans</i>	<i>dambrensis</i> , <i>occidentalis</i> , <i>elegans south</i> , <i>elegans north</i>
	<i>Galidictis fasciata</i>	<i>fasciata</i> , <i>striata</i>
	<i>Galidictis grandidieri</i>	NA
	<i>Mungotictis decemlineata</i>	<i>decemlineata</i> , <i>lineata</i>
	<i>Salanoia concolor</i>	NA
	<i>Salanoia durrelli</i>	NA
Felidae	<i>Acinonyx jubatus</i>	<i>hecki</i> , <i>raineyi</i> , <i>jubatus</i> , <i>soemmerringi</i> , <i>venaticus</i>
	<i>Caracal aurata</i>	<i>aurata</i> , <i>celidogaster</i> , <i>cottoni</i>
	<i>Caracal caracal</i>	<i>algira</i> , <i>caracal</i> , <i>damarensis</i> , <i>limpopoensis</i> , <i>lucani</i> , <i>michaelis</i> , <i>nubicus</i> , <i>poecilotis</i> , <i>schmitzi</i>
	<i>Felis chaus</i>	<i>affinis</i> , <i>chaus</i> , <i>furax</i> , <i>fulvidina</i> , <i>kutas</i> , <i>kelaarti</i> , <i>maimanah</i> , <i>nilotica</i> , <i>oxiana</i> , <i>prateri</i>
	<i>Felis margarita</i>	<i>harrisoni</i> , <i>margarita</i> , <i>scheffeli</i> , <i>thinobius</i>
	<i>Felis nigripes</i>	<i>nigripes</i> , <i>thomasi</i>
	<i>Felis silvestris</i>	<i>grampia</i> , <i>caucasica</i> , <i>jordansi</i> , <i>silvestris</i> , <i>tartessia</i> , <i>cafra</i> , <i>chutuchta</i> , <i>lybica</i> , <i>ocreata</i> , <i>rubida</i> , <i>griselda</i> , <i>mellandi</i> , <i>ornata</i> , <i>nesterovi</i> , <i>iraki</i>
	<i>Felis bieti</i>	NA
	<i>Felis catus</i>	" <i>catus</i> , <i>mummy</i> "
	<i>Leopardus colocolo</i>	<i>colocolo</i> , <i>budini</i> , <i>garleppi</i> , <i>pajeros</i> , <i>steinbachi</i> , " <i>northchile</i> ", <i>braccatus</i> , <i>munoi</i>
	<i>Leopardus geoffroyi</i>	<i>euxanthus</i> , <i>paraguae</i> , <i>salinarum</i> , <i>geoffroyi</i> , <i>leucobaptus</i>
	<i>Leopardus guigna</i>	<i>guigna</i> , <i>tigrillo</i>
	<i>Leopardus jacobita</i>	NA
	<i>Leopardus mitis</i>	<i>aequatorialis</i> , <i>mearni</i> , <i>melanura</i> , <i>mitis</i> , <i>pseudopardalis</i> , <i>pusaesus</i> , <i>steinbachi</i>
	<i>Leopardus pardalis</i>	<i>albescens</i> , <i>nelsoni</i> , <i>pardalis</i> , <i>sonoriensis</i>
	<i>Leopardus tigrinus</i>	NA
	<i>Leopardus guttulus</i>	NA
	<i>Leopardus pardinoides</i>	<i>pardinoides</i> , <i>oncilla</i>
	<i>Leopardus wiedii</i>	<i>wiedii</i> , <i>amazonicus</i> , <i>boliviae</i> , <i>cooperi</i> , <i>glauculus</i> , <i>nicaraguae</i> , <i>oaxacensis</i> , <i>pirrensis</i> , <i>salvinius</i> , <i>vigens</i> , <i>yucatanicus</i>
	<i>Leptailurus serval</i>	<i>beirae</i> , <i>brachyurus</i> , <i>constantinus</i> , <i>hamiltoni</i> , <i>hindei</i> , <i>ingridi</i> , <i>kempi</i> , <i>kivuensis</i> , <i>lipostictus</i> , <i>lombbergi</i> , <i>mababiensis</i> , <i>phillipsi</i> , <i>pococki</i> , <i>robertsi</i> , <i>serval</i> , <i>taanae</i> , <i>togoensis</i>

Family	Species	Subspecies considered for initial classification
Felidae	<i>Lynx canadensis</i>	<i>canadensis, mollipilosus, subsolanus</i>
	<i>Lynx lynx</i>	<i>lynx, carpathicus, balcanicus, dinniki, isabellinus, wardi, kozlovi, wrangeli, stroganovi</i>
	<i>Lynx pardinus</i>	<i>NA</i>
	<i>Lynx rufus</i>	<i>baileyi, californicus, escuinapae, fasciatus, floridanus, gigas, oaxacensis, pallescens, peninsularis, rufus, superiorensis, texensis</i>
	<i>Neofelis diardi</i>	<i>borneensis, diardi</i>
	<i>Neofelis nebulosa</i>	<i>brachyura, macrosceloides, nebulosa</i>
	<i>Otocolobus manul</i>	<i>manul, nigripsecta, ferruginea</i>
	<i>Panthera leo</i>	<i>persica, leo, senegalensis, azandica, nubica, bleyenberghi, krugeri</i>
	<i>Panthera onca</i>	<i>onca, peruviana, hernandesii, centralis, arizonensis, veracruzis, goldmani, palustris, paraguensis, paulensis</i>
	<i>Panthera pardus</i>	<i>pardus, fusca, melas, nimr, orientalis, japonensis, ciscaucasica, delacouri, kotiya, tulliana, sindica, panthera, jarvisi, adersi</i>
	<i>Panthera tigris</i>	<i>tigris, corbetti, jacksni, altaica, amoyensis, sumatrae, balica, virgata, sondaica</i>
	<i>Panthera uncia</i>	<i>baikalensis-romanii, schneideri, uncia, uncioides</i>
	<i>Catopuma badia</i>	<i>NA</i>
	<i>Catopuma marmorata</i>	<i>marmorata, charltoni</i>
	<i>Catopuma temminckii</i>	<i>temminckii, dominicanorum, tristis</i>
	<i>Prionailurus bengalensis</i>	<i>bengalensis, javanensis, sumatranus, chinensis, horsfieldi, euphilurus, borneoensis, trevelyani, alleni, iriomotensis, heaneyi, rabori</i>
	<i>Prionailurus planiceps</i>	<i>NA</i>
	<i>Prionailurus rubiginosus</i>	<i>phillipsi, koladivinus, rubiginosus</i>
	<i>Prionailurus viverrinus</i>	<i>risophores, viverrinus</i>
	<i>Puma concolor</i>	<i>cabrerai, costaricensis, anthonyi, cougar, concolor, puma, coryi</i>
	<i>Puma yagouaroundi</i>	<i>yagouaroundi, ameghinoi, cacomitli, eyra, fossata, melantho, panamensis, tolteca</i>
Herpestidae	<i>Atilax paludinosus</i>	<i>guineensis, macrodon, mitis, mordax, paludinosus, pluto, robustus, rubellus, rubescens, spadiceus, transvaalensis</i>
	<i>Bdeogale crassicauda</i>	<i>crassicauda, nigrescens, puisa, tenuis</i>
	<i>Bdeogale jacksoni</i>	<i>NA</i>
	<i>Bdeogale nigripes</i>	<i>NA</i>
	<i>Bdeogale omnivora</i>	<i>NA</i>
	<i>Crossarchus alexandri</i>	<i>alexandri, minor</i>
	<i>Crossarchus ansorgei</i>	<i>ansorgei, nigricolor</i>
	<i>Crossarchus obscurus</i>	<i>NA</i>
	<i>Crossarchus platycephalus</i>	<i>NA</i>
	<i>Cynictis penicillata</i>	<i>bradfieldi, coombsi, penicillata</i>
	<i>Dologale dybowskii</i>	<i>NA</i>
	<i>Helogale hirtula</i>	<i>ahlselli, annulata, hirtula, lutescens, percivali, powelli, tenebrosa</i>
	<i>Helogale parvula</i>	<i>parvula, ivori, mimetra, nero, ruficeps, undulatus, varia</i>

Family	Species	Subspecies considered for initial classification
Herpestidae	<i>Urva brachyura</i>	<i>brachyura, rajah</i>
	<i>Urva edwardsii</i>	<i>edwardsi, ferruginea, lanka, nyula, grisea</i>
	<i>Galerella flavescens</i>	NA
	<i>Galerella nigrata</i>	<i>nigrata, shortridgei, anulata</i>
	<i>Urva fusca</i>	<i>flavidens, fusca, maccarthiae, phillipsi, rubidior, sicattus</i>
	<i>Herpestes ichneumon</i>	<i>aetyptiae, aithos, cafra, centralis, funestus, grandis, ichneumon, lademanni, mababiensis, mesos, numidicus, occidentalis, parvidens, sabiensis, sangronizi, widdringtonii</i>
	<i>Urva javanica</i>	<i>javanicus, exilis, peninsulae, tjerapai</i>
	<i>Urva auropunctata</i>	<i>birmanica, rubifrons, auropunctata, pallipes, siamensis</i>
	<i>Xenogale naso</i>	<i>microdon, naso</i>
	<i>Galerella ochracea</i>	<i>fulvidior, ochracea, perfulvida</i>
	<i>Galerella pulverulenta</i>	<i>basuticus, pulverulenta, punctatissimus, ruddi</i>
	<i>Galerella sanguinea south</i>	<i>bocagei, cauui, dasilvai, ignitoides, lancasteri, mossambica, swalius, ignitus, swinnyi</i>
	<i>Galerella sanguinea central</i>	<i>canus, galbus, gracilis, ibeae, melanura, mustela, mutgigella, orestes, parvipes, phoenicurus, proteus, rendilis, rufescens, saharae, sanguinea, ugandae, dentifer, granti, neumanni, bruneo-ochracea, conradi, emini, ererensis, erlangeri, flaviventris, , ruasae, schimperi, turstigi</i>
	<i>Urva semitorquata</i>	<i>semitorquata, uniformis, parva</i>
	<i>Urva smithii</i>	<i>smithi, thysanura, zeylanicus</i>
	<i>Urva urva</i>	<i>formosana, fusca, sinensis, urva</i>
	<i>Urva vitticollata</i>	<i>inornata, vitticollata</i>
	<i>Ichneumia albicauda</i>	<i>albicauda, loempo, grandis, loandae, ibeana, dialeucos</i>
	<i>Liberiictis kuhni</i>	NA
	<i>Mungos gambianus</i>	NA
	<i>Mungos mungo</i>	<i>adailensis, boorensis, colonus, fasciatus, gothneh, grisonax, macrurus, mungo, ngamiensis, pallidipes, rossi, senescens, somalicus, taenianotus, zebra, zebroides</i>
	<i>Paracynictis selousi</i>	<i>bechuanae, gnamiensis, selousi, sengaani</i>
	<i>Rhynchogale melleri</i>	<i>langi, melleri</i>
	<i>Suricata suricatta</i>	<i>iona, marjoriae, suricatta</i>
Hyaenidae	<i>Crocuta crocuta</i>	<i>crocuta, fisi, fortis, habessynica, kibonotensis, leontiewi</i>
	<i>Parahyaena brunnea</i>	<i>brunnea, melampus</i>
	<i>Hyaena hyaena</i>	<i>schillingsi, barbara, dubbah, hyaena, sultana, syriaca</i>
	<i>Proteles cristata</i>	<i>cristata, septentrionalis</i>
Nandiniidae	<i>Nandinia binotata</i>	<i>arborea, binotata, gerrardi, intensa</i>
Prionodontidae	<i>Prionodon linsang</i>	<i>fredericae, gracilis, interlinius, linsang</i>
	<i>Prionodon pardicolor</i>	<i>pardicolor, presina</i>
Viverridae	<i>Arctictis binturong</i>	<i>binturong, albifrons, penicillatus, whitei, pageli, gairdneri, niasensis, kerkhoveni, memglaensis</i>
	<i>Arctogalidia stigmatica</i>	NA

Family	Species	Subspecies considered for initial classification
Viverridae	<i>Arctogalidia trivirgata</i>	<i>trivirgata, trilineata, leucotis</i>
	<i>Chrotogale owstoni</i>	<i>NA</i>
	<i>Civettictis civetta</i>	<i>civetta, australis, congica, pauli, schwarzi, volkmanni</i>
	<i>Cynogale bennettii</i>	<i>bennettii, lowei</i>
	<i>Diplogale hosei</i>	<i>NA</i>
	<i>Genetta abyssinica</i>	<i>NA</i>
	<i>Genetta angolensis</i>	<i>hintoni, angolensis</i>
	<i>Genetta felina</i>	<i>NA</i>
	<i>Genetta boursloni</i>	<i>NA</i>
	<i>Genetta schoutedeni</i>	<i>schoutedeni, gleimi, zambesiana</i>
	<i>Genetta cristata</i>	<i>NA</i>
	<i>Genetta genetta</i>	<i>afra, senegalensis, balearica, genetta, granti, isabelae, pyrenaica, rhodanica, terraesanctae</i>
	<i>Genetta johnstoni</i>	<i>NA</i>
	<i>Genetta maculata</i>	<i>aequatorialis, deorum, maculata, matschiei, schraderi, soror, suahelica</i>
	<i>Genetta letabae</i>	<i>NA</i>
	<i>Genetta pardina</i>	<i>dubia, pardina</i>
	<i>Genetta piscivora</i>	<i>NA</i>
	<i>Genetta poensis</i>	<i>NA</i>
	<i>Genetta servalina</i>	<i>archeri, bettoni, lowei, schwarzi, servalina</i>
	<i>Genetta thierryi</i>	<i>NA</i>
	<i>Genetta tigrina</i>	<i>methi, tigrina</i>
	<i>Genetta victoriae</i>	<i>NA</i>
	<i>Hemigalus derbyanus</i>	<i>boiei, derbyanus, minor, sipora</i>
	<i>Macrogalidia musschenbroekii</i>	<i>NA</i>
	<i>Paguma larvata</i>	<i>annectens, chichingensis, grayi, hainana, intrudens, janetta, laniger, larvata, leucocephala, leucomystax, neglecta, nigriceps, ogilbyi, robustus, taivana, tylerii, wroughtoni</i>
	<i>Paradoxurus hermaphroditus</i>	<i>minor, hermaphroditus, "north india", bengal</i>
	<i>Paradoxurus musanga</i>	<i>musangus, javanicus</i>
	<i>Paradoxurus phillipinensis</i>	<i>lignicolor, phillipinensis</i>
	<i>Paradoxurus jerdoni</i>	<i>caniscus, jerdoni</i>
	<i>Paradoxurus zeylonensis</i>	<i>zeylonensis, montanus, stenocephalus</i>
	<i>Poiana leightoni</i>	<i>NA</i>
	<i>Poiana richardsonii</i>	<i>ochracea, richardsonii</i>
	<i>Viverra civettina</i>	<i>NA</i>
	<i>Viverra megaspila</i>	<i>NA</i>
	<i>Viverra tangalunga</i>	<i>lankavensis, tangalunga</i>
	<i>Viverra zibetha</i>	<i>ashtoni, hainana, picta, pruinosa, zibetha</i>
	<i>Viverricula indica</i>	<i>atchinensis, baliensis, baptistae, bengalensis, deserti, indica, klossi, mayori, muriavensis, pallida, schlegelii, thai, wellsii, rasse</i>