Adaptaciones anatómicas de la escápula y del manguito rotador a las diferentes formas de locomoción en el orden de los primates

Gaëlle Bello Hellegouarch

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UNIVERSITAT DE BARCELONA

ADAPTACIONES ANATÓMICAS DE LA ESCÁPULA Y DEL MANGUITO ROTADOR A LAS DIFERENTES FORMAS DE LOCOMOCIÓN EN EL ORDEN DE LOS PRIMATES

Memoria presentada por:

GAËLLE BELLO HELLEGOUARCH

Para optar al grado de

Doctor por la Universitat de Barcelona

Programa de Doctorado en *Biodiversidad* (2008-09)

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Los Directores

La Doctoranda

Dr. A. Martínez Pérez-Pérez

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Dr. J. M. Potau Ginés

A mi abueliña

"Ce livre est écrit beaucoup avec
le rêve, un peu avec le souvenir.
Rêver est permis aux vaincus;
se souvenir est permis aux solitaires."

Victor Hugo

"You did this, you bloody baboon!"

Planet of the Apes, 1968

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“The scapula in the living form is suspended, as it were, in space by the muscles acting upon it, and it is, therefore, not surprising that this bone should reflect more clearly than any other the changes which have been brought about by more specialized functional demands.”

Inman *et al*., 1944: 2

I. Introducción

1. ORDEN PRIMATES

1.1. Características principales

El orden de los Primates se caracteriza por su enorme diversidad (*Figura 1*). Es, dentro de los mamíferos, el orden con mayor variabilidad en los sistemas de locomoción y los sistemas sociales (Ankel-Simons 2007). Actualmente se conocen unos 60 géneros con 376 especies (Groves 2005), lista que aumenta progresivamente tras los continuos descubrimientos de nuevas especies. Esta enorme variabilidad es el resultado de la radiación de los Euprimates (primates de aspecto moderno) que tuvo lugar hace unos 55 m.a., durante el Eoceno temprano (Ni *et al*. 2004). Para que esta radiación tuviera lugar, fue fundamental la exitosa explotación del medio arbóreo (Nowak 1999; Garber 2007; Vaughan *et al*. 2010). El primate actual más pequeño que se conoce es el lémur ratón de Berthe (*Microcebus berthae*) con unos 30 g de peso, mientras que el gorila es el primate actual conocido más grande, con un peso de alrededor de 200 kg (*Figura 2*). La mayoría de los primates, a excepción de los humanos que se encuentran repartidos en todos los continentes, viven en las regiones tropicales y subtropicales de América, África y Asia, la mayoría de ellos en medios arbóreos (Fleagle 1999; Ankel-Simons 2007; Vaughan *et al*. 2010).

El orden de los Primates se diversificó en hábitats arbóreos, por lo que muchos de los rasgos que lo caracterizan surgieron probablemente como adaptaciones a la vida en los árboles (rostro acortado y órbitas orientadas hacia adelante, asociados con la visión estereoscópica; aumento de tamaño y complejidad del cerebro;

hallux y *pollex* oponibles; ulna y radio no fusionados y con gran movilidad; tibia y fíbula no fusionadas y altamente móviles) o son caracteres primitivos que se conservaron por la misma razón (Martin 1990; Ankel-Simons 2007).

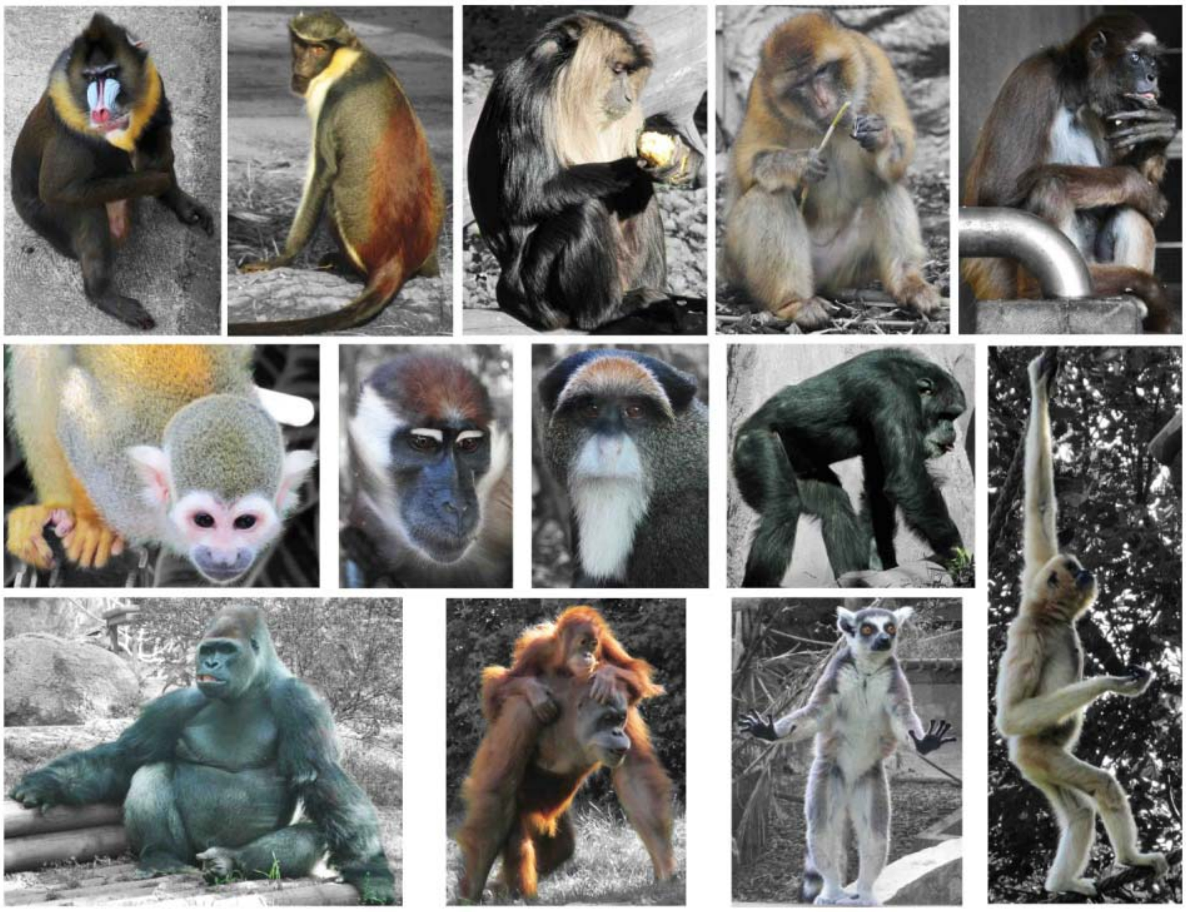

***Figura 1.** Variabilidad del orden de los Primates. De arriba a abajo y de izquierda a derecha*: Mandrillus sphinx, Cercopithecus diana, Macaca silenus, Macaca sylvanus, Ateles hybridus, Saimiri sciureus, Cercocebus torquatus, Cercopithecus neglectus, Pan troglodytes, Gorilla gorilla, Pongo pygmaeus, Lemur catta, Hylobates lar *(todas las fotografías realizadas por la autora).*

Algunas especies, incluida la nuestra, abandonaron el medio arbóreo para vivir en el suelo, manteniendo aún muchas de estas características. Sin embargo, comparados con el resto de los mamíferos (ver, por ejemplo, las alas de los murciélagos, la reducción de dedos de los caballos o las adaptaciones extremas de las ballenas), los primates han retenido muchos caracteres primitivos (Martin 1990), por lo que algunas de sus características anatómicas son el resultado de cambios sutiles en la forma y proporción de elementos homólogos. Resulta complicado definir de forma precisa este orden, debido a que la mayoría de características anatómicas del esqueleto constituyen una mezcla de rasgos primitivos y derivados, especialmente del cráneo, dientes y extremidades (Martin 1990; Fleagle 1999; Ankel-Simons 2007; Vaughan *et al*. 2010).

Características comunes a los primates son la pentadactilia (con algunos casos de reducción o incluso desaparición de los pulgares), los pies plantígrados, la presencia de clavícula, una gestación prolongada, la presencia de pulgares oponibles en manos y pies, órbitas rodeadas de un anillo óseo, visión en color (con algunas excepciones) y estereoscópica, hemisferios cerebrales desarrollados, presencia de uñas planas en lugar de garras (con algunas excepciones, como los callitrícidos, que tienen garras por adaptación secundaria al desplazamiento por troncos de gran tamaño), dentición poco especializada (en prosimios y platirrinos: 2 incisivos, 1 canino, 3 ó 2 premolares y 3 molares en cada hemimaxila; en catarrinos: 2 incisivos, 1 canino, 2 premolares y 3 molares en cada hemimaxila) y un estómago simple (saculado en algunos cercopitécidos folívoros). También existe en los primates una tendencia hacia la reducción de la región olfatoria del cerebro y la expansión del encéfalo relacionada con el incremento de la importancia de la visión y de comportamientos sociales complejos.

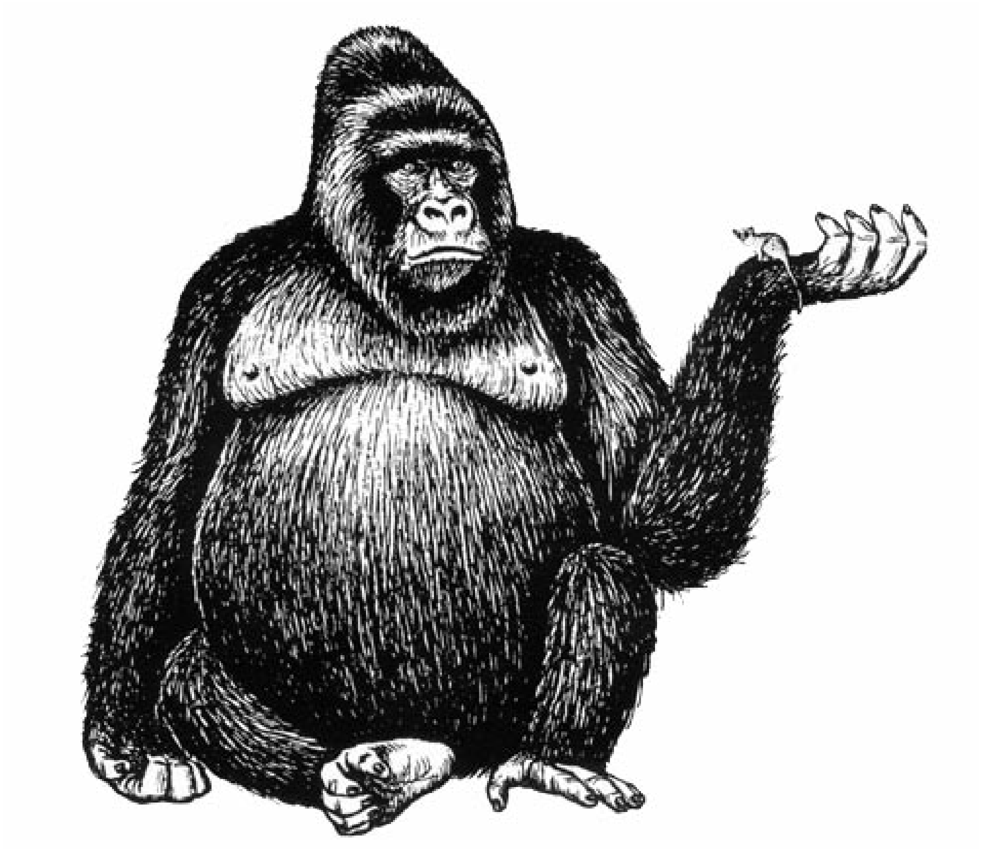

Figura 2. *Lémur ratón (*Microcebus*) en la mano de un gorila (*Gorilla*), respectivamente, el primate más pequeño y el más grande que existen actualmente (adaptada de Fleagle 1999).*

Históricamente los Primates se dividían en dos grupos principales: Prosimii y Anthropoidea (Simpson 1945). Los **Prosimios** comparten caracteres ancestrales de los primeros primates, siendo más generalizados, morfológicamente hablando, que los que presentan los Antropoideos (Martin 1990); incluyen los lemúridos, lorísidos, gálagos y társidos. Los **Antropoideos**, monos y simios (incluyendo los homininos), muestran rasgos más especializados o derivados. Sin embargo actualmente esta clasificación no está plenamente aceptada (Groves 2001) por no ser cladísticamente correcta (los Prosimios constituyen un grupo parafilético), teniendo actualmente mayor reconocimiento la división en los subórdenes Strepsirrhini y Haplorhini por ser grupos monofiléticos (*Figura 3*).

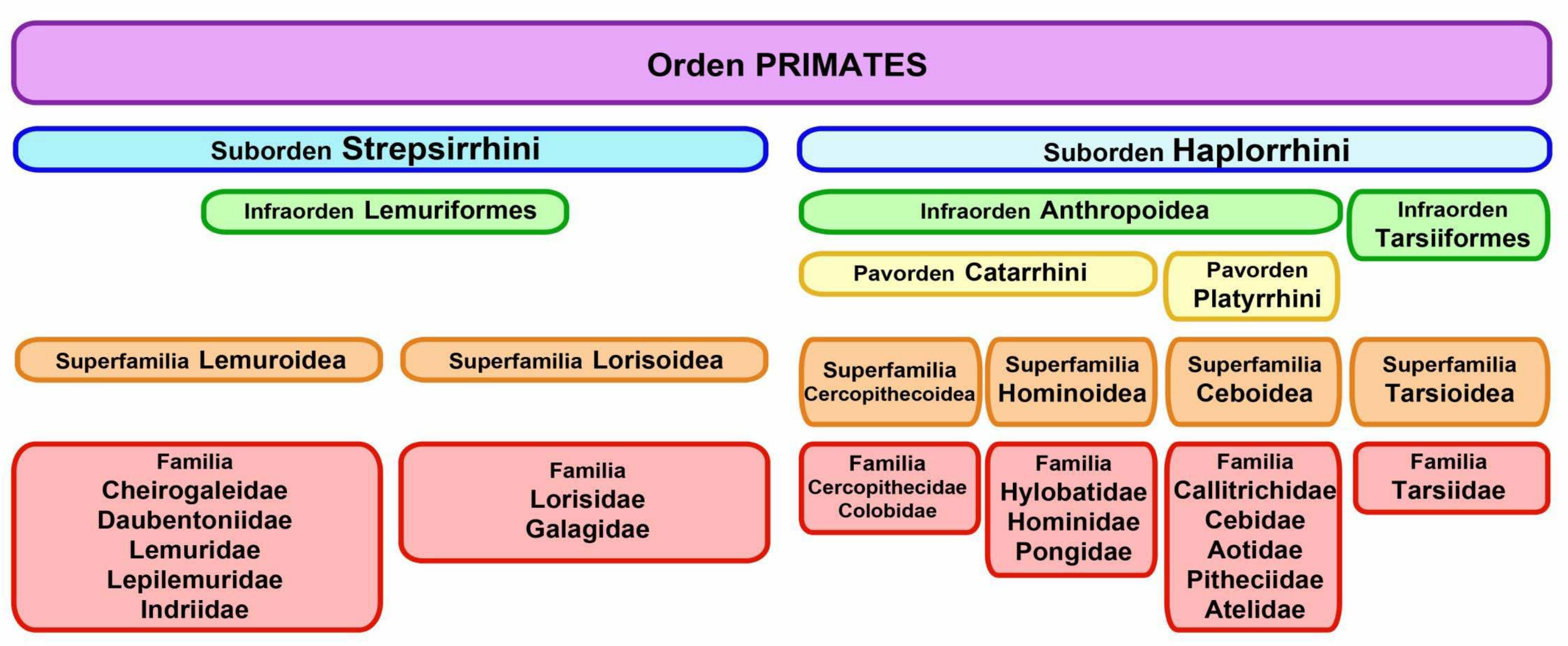

Figura 3. *Clasificación del orden de los Primates hasta el nivel de las familias actuales (según Cartmill 2010).*

El suborden **Strepsirrhini** (*Figuras 3 y 4*) incluye todos los prosimios excepto los társidos: las cinco familias de lémures endémicas de Madagascar (Cheirogaleidae, Lemuridae, Lepilemuridae, Indriidae y Daubentoniidae), la familia Galagidae de África, y la familia Lorisidae de África y Sudeste Asiático (Cartmill 2010; Vaugham *et al*. 2010). Los primates estrepsirrinos se caracterizan por tener un rhinario húmedo con vibrisas en el hocico, típico de muchos otros mamíferos (Andrews 1988), conectado con la boca a través de un labio partido.

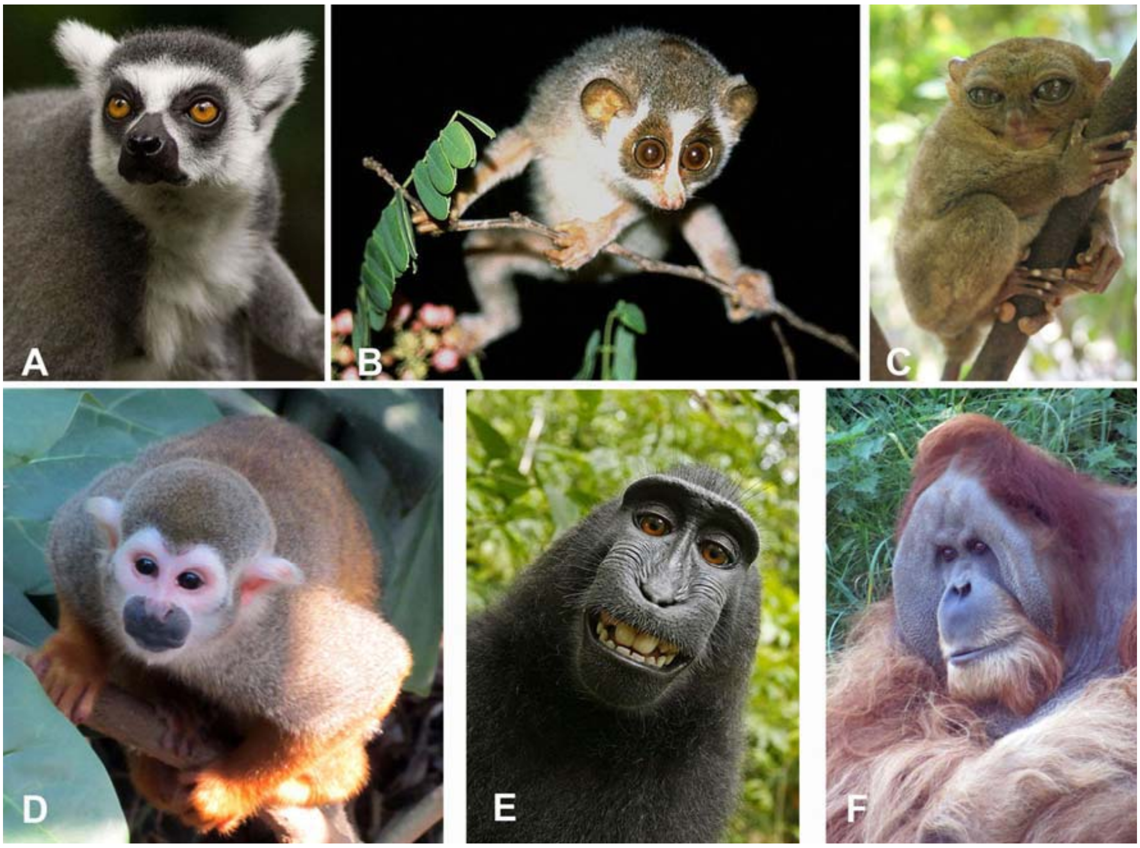

Figura 4. *Especies representativas de los diferentes taxones del orden de los Primates.* ***A:*** Lemur catta*,* ***B:*** Loris lydekkerianus *(imagen realizada la Dr. K.A.I. Nekaris),* ***C:*** Tarsius syrichta*,* ***D:*** Saimiri sciureus*,* ***E:*** Macaca nigra*,* ***F:*** Pongo pygmaeus*. A (Lemuridae) y B (Lorisidae) son representantes del suborden Strepsirrhini, mientras que C (Tarsiidae), D (Platyrrhini, Cebidae), E (Cercopithecidae) y F (Pongidae) son representantes del suborden Haplorhini.*

El suborden **Haplorhini** (*Figuras 3 y 4*) incluye la familia Tarsiidae y los primates antropoideos del Nuevo y Viejo Mundo. A diferencia de los primates estrepsirrinos, los haplorrinos carecen del rhinario y de vibrisas en el hocico. Además de la familia Tarsiidae, el suborden Haplorrhini se divide en dos grupos: Platyrrhini (Nuevo Mundo) y Catarrhini (Viejo Mundo). Los Platirrinos tienen el septo nasal aplastado, con los orificios nasales orientados hacia fuera, mientras que en los Catarrinos se orientan hacia abajo. Los **Platyrrhini** incluyen cinco familias: Callitrichidae (titís y tamarinos), Cebidae (capuchinos y monos ardilla), Aotidae (monos lechuza), Pitheciidae (sakis y uakaris) y Atelidae (monos araña, monos aulladores, monos lanudos). Los **Catarrhini** incluyen las familias Cercopithecidae (macacos, papiones, mangabeys, etc.), Colobidae (colobos y langures), Hylobatidae (gibones y siamang), Pongidae (orangutanes) y Hominidae (gorilas, chimpancés y humanos) (Cartmill 2010).

1.2. Pronógrados *vs*. Ortógrados

En función del plan corporal del esqueleto post-craneal el orden de los Primates se divide en dos grupos: pronógrados y ortógrados.

El plan corporal **pronógrado** (*Figura 5* y *6*) está presente en la mayoría de los primates excepto en los hominoideos, como en la mayoría de los mamíferos cuadrúpedos. Se caracteriza por un tórax ancho dorsoventralmente (Gebo 2010) orientado en posición horizontal durante la locomoción, con las extremidades anteriores situadas ventralmente y las escápulas posicionadas en el plano parasagital en la región lateral del tórax (la cavidad glenoidea se orienta ventralmente) y la cabeza y la cola se sitúan en los extremos del cilindro (Fleagle 1999; Gebo 2010).

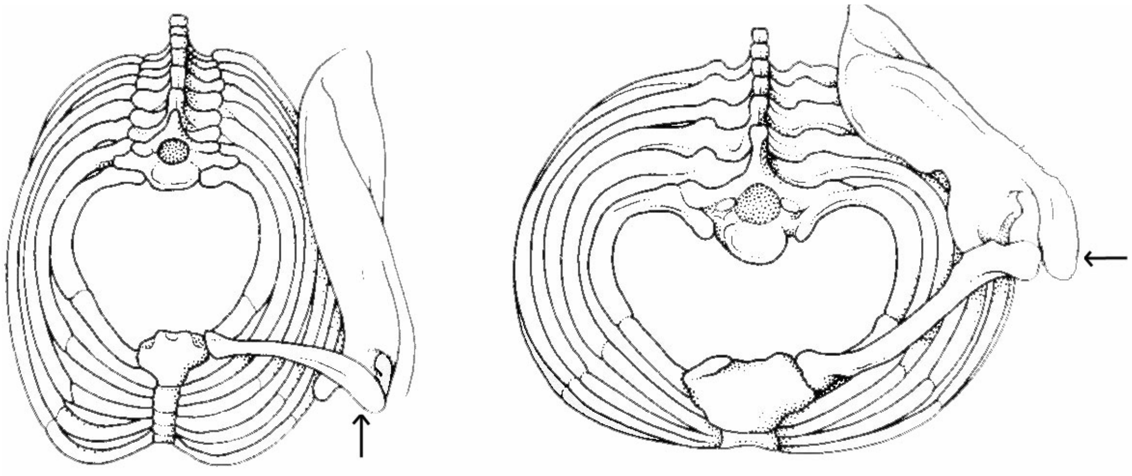

Figura 5. *Vista anteroposterior del tórax y articulación del hombro de macaco (patrón corporal pronógrado, a la izquierda) y de humano (patrón corporal ortógrado, a la derecha). Se observa la orientación diferente de la articulación glenohumeral (flechas), la diferente ubicación de la escápula en relación con las costillas y las diferencias en el contorno de la caja torácica (adaptada de Aiello & Dean 1990).*

El plan corporal **ortógrado** *(Figuras 5 y 6)*, propio de los hominoideos (incluidos los humanos), se caracteriza por un tórax estrecho dorsoventralmente y ancho en sentido mediolateral, orientado en posición vertical durante la locomoción, y por la ausencia de cola (Aiello & Dean 1990; Larson 1993; Gebo 2010). Los hombros se encuentran desplazados a ambos lados del cuerpo y las escápulas se sitúan dorsalmente en el tórax, en lugar de a ambos lados de la caja torácica. Esta posición de las escápulas aleja los hombros del eje central del cuerpo y orienta la cavidad glenoidea ventrolateralmente (Keith 1923; Schultz 1930; Ward 2007), forzando al húmero a sufrir una torsión medial con el fin de que se articule con la escápula al mismo tiempo que el codo se orienta dorsoventralmente (Aiello & Dean 1990; Larson 1993; Gebo 2010). Esta orientación lateral de la cavidad glenoidea aumenta la movilidad de la articulación glenohumeral, permitiendo la libre elevación de la mano por encima de la escápula (Roberts 1974; Larson 1993). Todos estos caracteres están relacionados con la adaptación a la locomoción en un medio arbóreo, en el que el movimiento a través del dosel se realiza debajo de las ramas, fundamentalmente con las extremidades anteriores, que requieren gran libertad de movimiento.

Es importante no confundir el *plan corporal ortógrado* con la *postura ortógrada*. Numerosos primates pronógrados pueden adoptar una postura ortógrada (esto es, vertical, con la espalda erecta) en caso de necesidad (por ejemplo, durante el *climbing*), aunque presentan los caracteres anatómicos del plan corporal pronógrado.

1.3. Tipos de locomoción

La **locomoción**, definida como el conjunto de movimientos realizados para desplazarse a través del hábitat, es un componente fundamental en la adaptación anatómica del esqueleto post-craneal de cualquier mamífero (Martin 1990). El orden de los Primates es, dentro de los mamíferos, el orden con mayor diversidad de la morfología post-craneal en relación con los patrones locomotores (Cant 1992; Cant *et al*. 2001; Ankel-Simons 2007; Garber 2007) y su exitosa radiación en los bosques tropicales. Esta radiación es un reflejo de las diferencias en el modo en el que las diferentes especies de primates explotan los hábitats tridimensionales (Nowak 1999; Garber 2007; Vaughan *et al*. 2010). Esta gran diversidad de comportamientos locomotores dificulta la asociación de una determinada especie de primate a una única categoría locomotora, existiendo numerosas discusiones en la literatura acerca de cómo conseguir una categorización comportamental precisa (Prost 1965; Napier & Napier 1967; Rose 1973; Hunt *et al*. 1996; Wright-Fitzgerald *et al*. 2010).

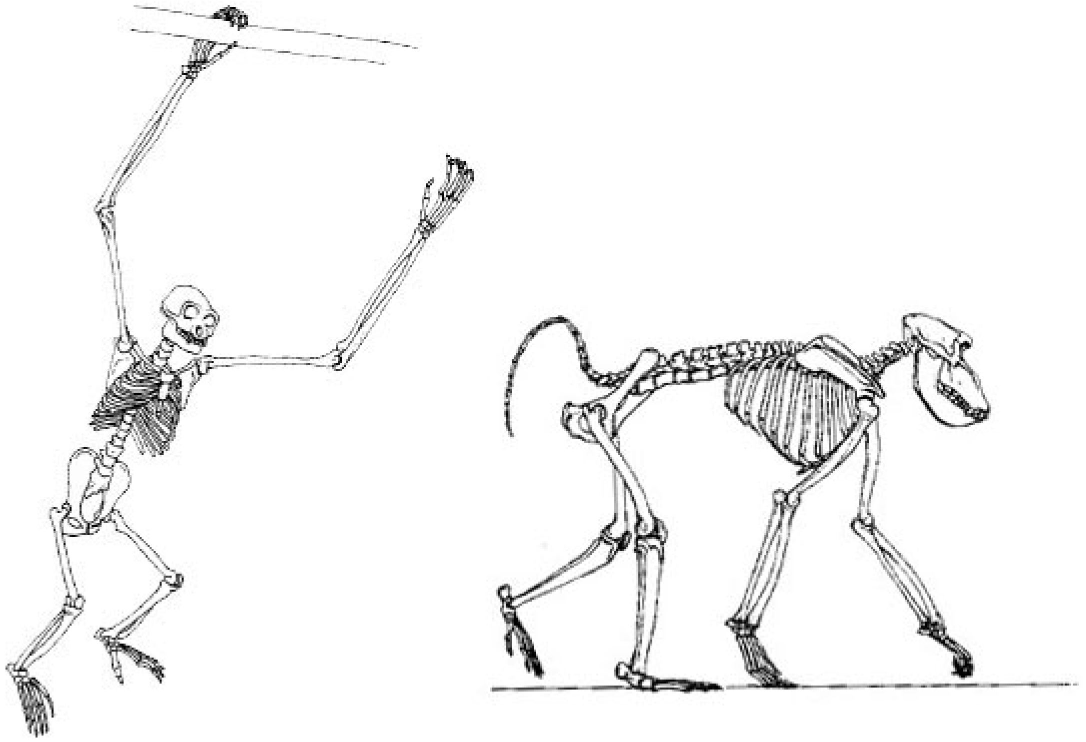

Figura 6. *Patrón corporal ortógrado (izquierda) y pronógrado (derecha). En el esqueleto ortógrado la escápula se sitúa dorsalmente, la cavidad glenoidea se orienta cranealmente y el tórax es ancho, mientras que el esqueleto del primate pronógrado se caracteriza por un tórax estrecho y una escápula situada lateralmente en el plano parasagital con la cavidad glenoidea orientada ventralmente (ambas imágenes adaptadas de Fleagle 1999).*

Frecuentemente se emplean categorías locomotoras para facilitar el análisis de los datos (Martin 1990), aunque no son estrictamente exactas y no hacen justicia a la diversidad real de la enorme variabilidad locomotora de los primates (Martin 1990; Fleagle 1999; Ankel-Simons 2007), basadas en la frecuencia de tiempo empleado en un determinado comportamiento (Wright-Fitzgerald *et al*. 2010). La mayoría de las especies muestran tendencias locomotoras en función del tamaño corporal, la dieta, el clima, el sustrato, los tipos de bosques por los que se mueven e incluso de la altura del dosel arbóreo en el que pasan la mayor parte del tiempo (Charles-Dominique 1990; Fleagle 1999; Nowak 1999; Ankel-Simons 2007). Debido a esto, la mayoría de los primates se pueden asignar de modo general a los siguientes tipos no excluyentes de locomoción: cuadrupedia arbórea, cuadrupedia terrestre, *climbing*, *pronograde clambering*, *leaping*, *vertical clinging*, suspensión (que incluye suspensión cuadrúpeda, *arm-swinging,* braquiación) y bipedismo (Hunt *et al*. 1996; Fleagle 1999; Nowak 1999; Ankel-Simons 2007; Schmidt 2010).

1.3.1. Cuadrupedia arbórea

La cuadrupedia arbórea es la locomoción más común entre los primates actuales y probablemente el modo de locomoción ancestral de los primeros primates (Rose 1973; Martin 1990; Fleagle 1999; Nowak 1999; Schmitt 2003; Schmidt 2010). Consiste en la progresión sobre las pequeñas ramas de los árboles empleando las cuatro extremidades (Rose 1973; Fleagle 1999; Schmidt 2010).

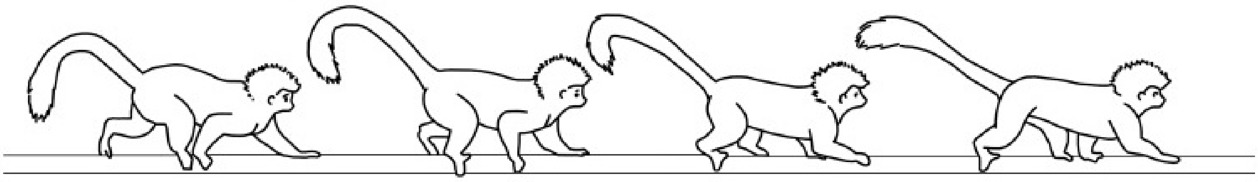

Figura 7. *Progresión mediante cuadrupedia arbórea (adaptada de Schmidt 2010).*

Los primates cuadrúpedos arbóreos (Figura 7) se enfrentan a sustratos discontinuos, poco estables, cilíndricos y de tamaño, inclinación y capacidad de soportar peso variables, por lo que comparten adaptaciones destinadas a mantener el equilibrio sobre ramas relativamente pequeñas e inestables (Cartmill 1974; Cartmill & Milton 1977; Grand 1984; Cant 1992; Dunbar & Badam 2000; Garber 2007).

Figura 8. Nycticebus *realizando* slow-climbing quadrupedalism *(imagen realizada por Frans Lanting, publicada en* The Guardian*).*

Este modo de locomoción presenta numerosas variantes entre los primates. Los lorísidos, por ejemplo, realizan movimientos muy lentos y deliberados conocidos como *slow-climbing quadrupedalism*, *tardigrady*, o *lorisine crawling* (*Figura 8*), una progresión en la que suele estar involucrada una única extremidad en cada momento (Napier & Napier 1967; Walker 1974; Gebo 1987, 1989; Jouffroy 1989; Demes *et al*. 1990; Hunt *et al*. 1996; Runestad 1997; Schmidt 2010).

1.3.2. Cuadrupedia terrestre

El desplazamiento por el suelo (*Figura 9*), un sustrato mucho más uniforme y estable que el arbóreo (Rose 1973; Fleagle 1999; Garber 2007), es un modo de locomoción poco frecuente en primates, aunque es característico de monos del Viejo Mundo de gran tamaño (Fleagle 1999; Schmidt 2010).

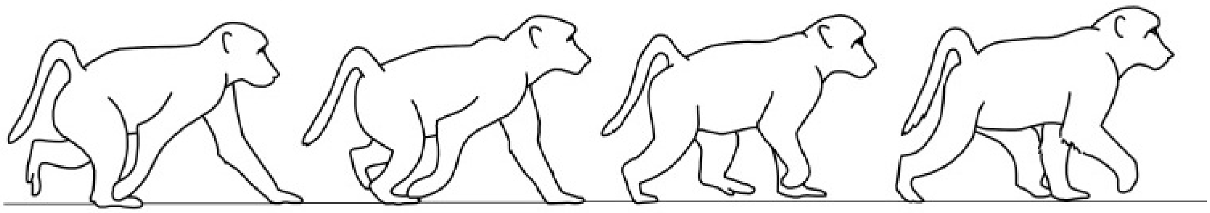

Figura 9. *Progresión mediante cuadrupedia terrestre (adaptada de Schmidt 2010).*

Un modo especial de cuadrupedia terrestre es el *knuckle-walking* (*Figura 10*) realizado por los grandes simios africanos (Hunt 1992; Doran 1996; Hunt *et al*. 1996; Fleagle 1999; Richmond *et al*. 2001). Durante el *knuckle-walking* el peso de las extremidades anteriores recae en la cara dorsal de las falanges medias de los dedos (Aiello & Dean 1990; Fleagle 1999; Gebo 2010), principalmente los dedos III y IV en el chimpancé (Tuttle 1967) y II a IV en el gorila (Tuttle 1969). Este modo de locomoción permite a estos primates emplear las manos en la cuadrupedia terrestre manteniendo, al mismo tiempo, unos dedos largos adaptados a comportamientos locomotores arbóreos (Gebo 2010).

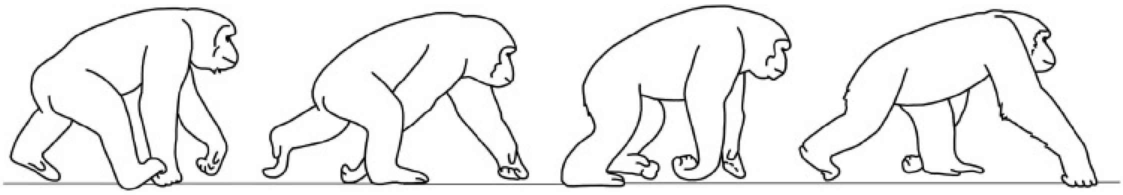

Figura 10. *Progresión mediante* knuckle-walking *(adaptada de Schmidt 2010).*

El *knuckle-walking* llevado a cabo por gorilas y chimpancés no es idéntico (Kivell & Schmitt 2009), siendo el de los gorilas más "columnar", de modo que la mano y la articulación de la muñeca se encuentran alineadas en una postura relativamente recta, neutra, mientras que los chimpancés realizan el *knuckle-walking* con la extremidad y la muñeca más extendidas. Esta diferencia se puede atribuir a la mayor frecuencia de tiempo que emplean los chimpancés en comportamientos arbóreos en comparación con los gorilas (Kivell & Schmitt 2009).

Figura 11. Climbing *(adaptada de Hunt* et al*. 1996).*

1.3.3. *Climbing*

El *climbing* es un modo de locomoción omnipresente en todos los primates actuales (*Figura 11*), mediante el cual emplean las cuatro extremidades para ascender o descender de los soportes arbóreos verticales (Mittermeier & Fleagle 1976; Gebo 1996; Hunt *et al*. 1996; Schmidt 2010).

1.3.4. Pronograde clambering

El *pronograde clambering* consiste en una progresión cuadrúpeda arbórea carente de una marcha regular (*regular gait*). Se realiza en soportes irregulares de diferentes tamaños e inclinaciones. Es típico, por ejemplo, de los monos aulladores (Schön Ybarra 1987; Hunt *et al*. 1996; Cant *et al*. 2001).

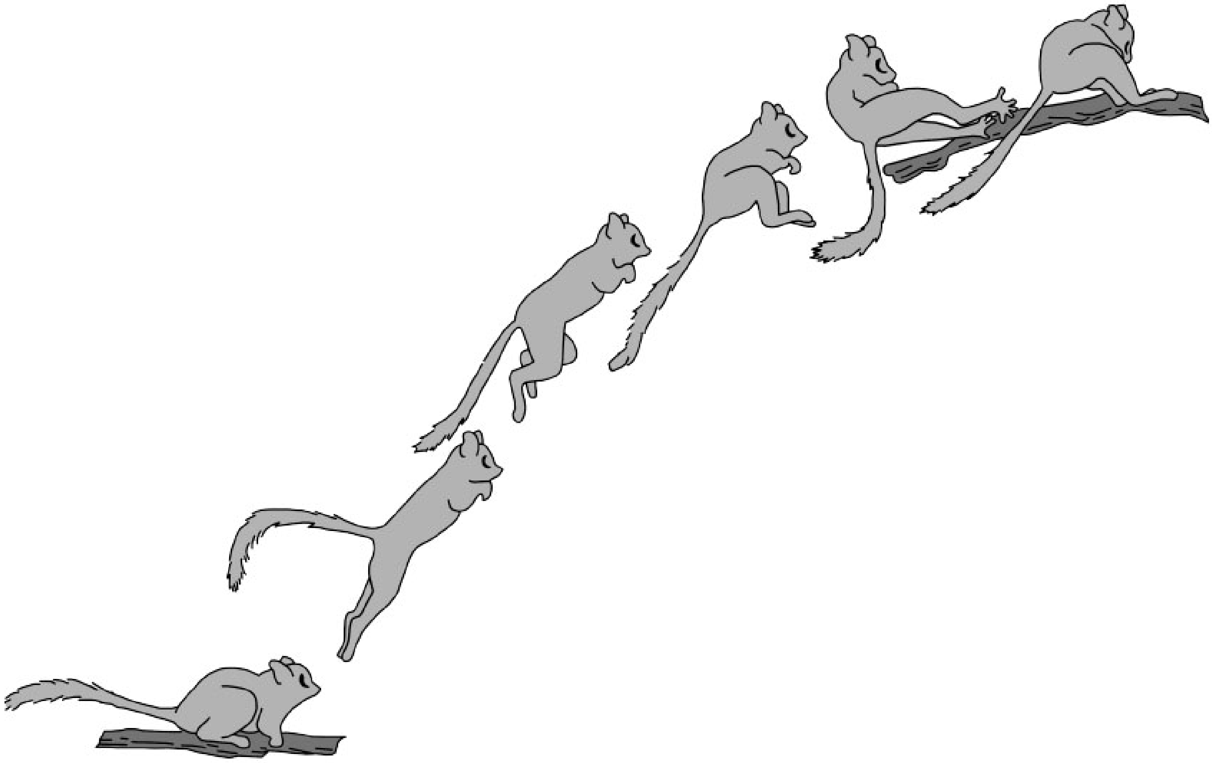

Figura 12. *Progresión mediante* leaping *(adaptada de Schmidt 2010).*

1.3.5. Leaping

El *leaping* es el modo de locomoción más rápido, empleado a menudo para huir de depredadores o para cruzar zonas abiertas (Hunt *et al*. 1996; Fleagle 1999; Nowak 1999; Schmidt 2010). El *leaping* consiste en cruzar distancias mediante el vuelo libre (*Figura 12*) entre sustratos, tanto verticales como horizontales o inclinados, mediante la rápida extensión de las extremidades posteriores (Ankel-Simons 2007; Schmidt 2010).

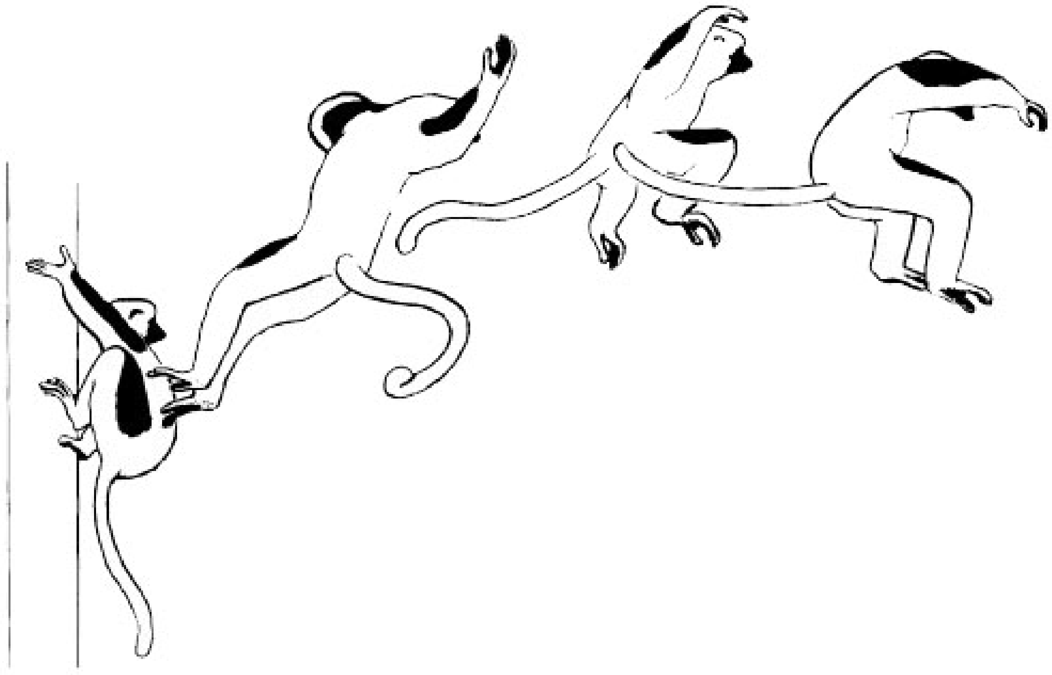

Figura 13. Vertical clinging and leaping *(adaptada de Demes* et al*. 1996).*

Las adaptaciones para este modo de locomoción han evolucionado de manera independiente en numerosas especies de primates (Terranova 1996; Fleagle 1999; Nowak 1999). Un modo extremadamente especializado de *leaping* es el conocido como ***vertical clinging and leaping*** *(Figura 13)*, realizado por los pequeños gálagos y társidos, y los indris de gran tamaño (Demes *et al*. 1996). Este tipo de locomoción se caracteriza por increíbles saltos, realizados principalmente con las extremidades posteriores, a través de enormes distancias en una posición parcialmente erecta (Napier & Walker 1967; Walker 1974; Gebo 1987; Hunt *et al*. 1996).

Esta categoría locomotora, sin embargo, no debe confundirse con la conocida como ***vertical clinging***, propia de muchos monos pequeños del Nuevo Mundo, como los titís y los tamarinos (Hunt *et al*. 1996; Ankel-Simons 2007; Schmidt 2010), que se caracteriza por el uso de las garras para aferrarse (*cling*) a las ramas anchas y los troncos verticales (Garber 1992; Ankel-Simons 2007).

1.3.6. Suspensión cuadrúpeda

La suspensión cuadrúpeda se caracteriza por el desplazamiento horizontal bajo el sustrato (mayoritariamente ramas) en una postura invertida (*dorsal-side down*) empleando las cuatro extremidades en tensión (*Figura 14*). Este modo de locomoción es típico de lorísidos y atélidos (Napier 1967; Hunt *et al*. 1996; Fujiwara *et al*. 2011).

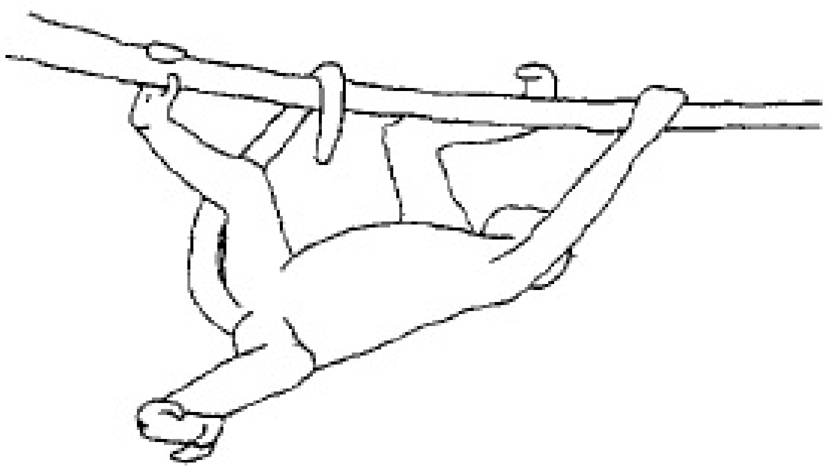

Figura 14. *Suspensión cuadrúpeda (adaptada de Mittermeier & Fleagle 1976).*

1.3.7. Suspensión bimanual

La suspensión bimanual presenta varias modalidades, siendo las más conocidas el ***arm-swinging*** (*Figura 15*) y la **braquiación,** diferenciadas por la escasa o elevada rotación del tronco, respectivamente. Se caracteriza por la progresión a dos manos por debajo del soporte arbóreo, permitiendo a especies de gran tamaño desplazar su peso corporal entre pequeños soportes (Mittermeier & Fleagle 1976; Jenkins *et al*. 1978; Jungers & Stern 1981; Hunt *et al*. 1996; Fleagle 1999; Cant *et al*. 2003).

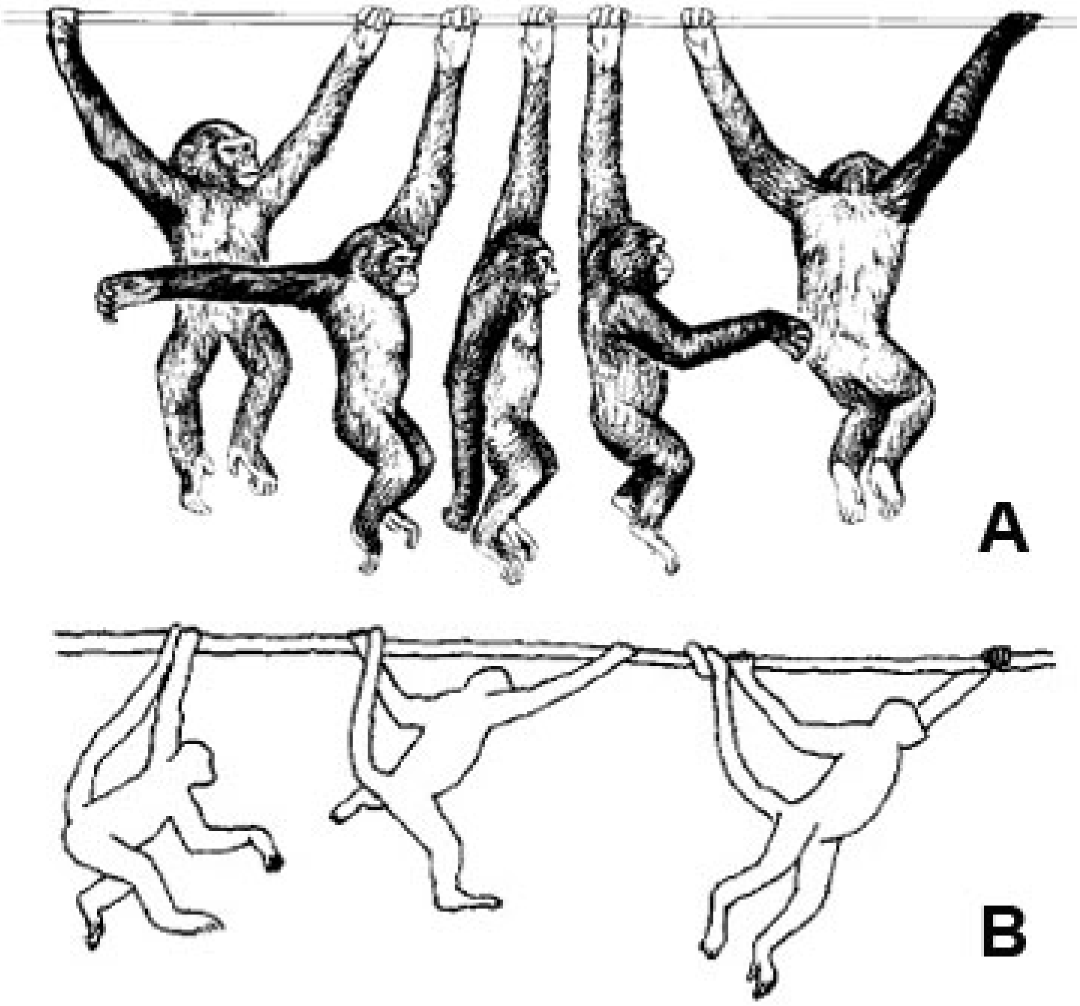

Figura 15. *Suspensión bimanual. A:* arm-swinging *realizado por chimpancés (adaptado de Larson & Stern 1986). B: suspensión bimanual típica de atélidos, en la que se aprecia el uso de la cola prensil como quinta extremidad (adaptada de Mittermeier & Fleagle 1976).*

Este modo de locomoción lo realiza un número muy limitado de primates, como los hominoideos (especialmente los hilobátidos), los monos araña (*Ateles*) y, en menor medida, los monos lanudos

(*Lagothrix*). Los monos del Nuevo Mundo que realizan este tipo de locomoción (*Figura 15B*) se diferencian de los simios (*Figura 15A*) en que emplean la cola prensil como quinta extremidad durante el desplazamiento (Hunt *et al.* 1996; Cant *et al*. 2001, 2003; Kagaya 2007; Schmidt 2010).

Existe cierta confusión en la literatura sobre el uso de los términos **braquiación** y ***arm-swinging*** (Erikson 1963; Napier 1963; Ashton & Oxnard 1964; Napier & Napier 1967; Andrews & Groves 1976; Jenkins *et al*. 1978; Jungers & Stern 1981; Rollinson & Martin 1981; Cant *et al*. 2003; Ankel-Simons 2007). Generalmente el término *braquiación* se emplea exclusivamente para la locomoción denominada ***ricochetal arm-swinging***, propia de los hilobátidos (gibones y siamang), durante la cual el cuerpo pasa por una fase de vuelo libre (sin contacto con el sustrato) y una fase de agarre al sustrato (véase Trevor 1963). El término *arm-swinging* se emplea para el resto de comportamientos suspensores (Rollinson & Martin 1981; Ankel-Simons 2007). Sin embargo, algunos autores emplean el término *braquiación* como sinónimo en cualquier tipo de locomoción suspensora con algún tipo de *arm-swinging*, incluyendo en el grupo de los braquiadores al orangután, al chimpancé e, incluso, a los gorilas. La *suspensión bimanual* llevada a cabo por los atélidos suspensores (*Ateles* y *Lagothrix*) ha sido clasificada indistintamente como braquiación, semibraquiación o *arm-swinging* (Erikson 1963; Napier 1963; Ashton & Oxnard 1964; Napier & Napier 1967; Andrews & Groves 1976; Mittermeier & Fleagle 1976; Aiello & Dean 1990).

1.3.8. Bipedismo

El bipedismo, casi exclusivo de la especie humana (*Figura 16*), consiste en el desplazamiento con las extremidades posteriores, que soportan todo el peso corporal (Gebo 2010). Esta adaptación locomotora supuso un drástico reajuste de la morfología y función del esqueleto post-craneal, quedando las extremidades anteriores liberadas para su uso en otras tareas, como la manipulación de objetos.

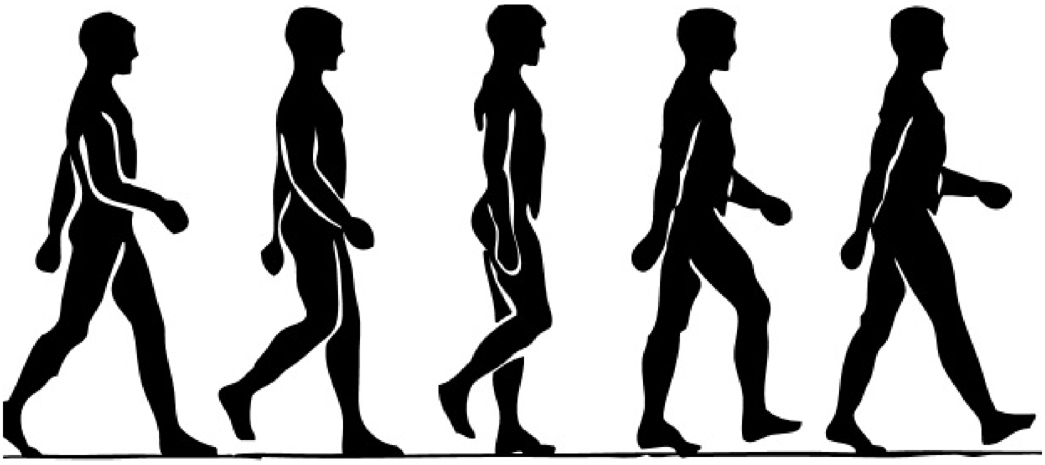

Figura 16. *Progresión mediante bipedismo.*

2. ANATOMÍA DEL HOMBRO

La evolución de los primates se caracteriza por cambios significativos en la función de las extremidades anteriores, que se fueron volviendo menos relevantes para soportar el peso corporal y más importantes a la hora de proporcionar estabilidad, agarre y manipulación en un medio arbóreo discontinuo, aumentando su movilidad y precisión (Rose 1973; Larson 1998; Schmitt 1998; Schmitt & Lemelin 2002; Lemelin & Schmitt 2007; Schmitt 2010). En este contexto, la función principal del hombro ha sido proporcionar la movilidad necesaria para alcanzar los soportes irregulares de ese sustrato arbóreo discontinuo, manteniendo al mismo tiempo una estabilización adecuada de la articulación glenohumeral con el fin de asegurar la estabilidad postural (Roberts 1974; Larson 1993; Schmidt & Krause 2011).

2.1. El manguito rotador

La necesidad de estabilización de la **articulación glenohumeral** es fácilmente comprensible al observar su anatomía (*Figura 17*). La *cavidad glenoidea* es la superficie que se articula con la cabeza del húmero, siendo la primera mucho más pequeña que la segunda (Terry & Chopp 2000; Jenkins 2009).

Para compensar la diferencia de tamaño, alrededor de la cavidad glenoidea se encuentra un anillo de fibrocartílago conocido como ***rodete (labrum) glenoideo***, que hace que la fosa sea amplia y profunda, estabilizando parcialmente la articulación glenohumeral. La estabilización de la articulación es especialmente importante durante movimientos que provocan fuerzas de tensión en la articulación, como es el caso de las actividades suspensoras. En esta situación, la estabilización de la articulación no sólo se mantiene mediante estructuras osteoligamentosas estáticas, sino también, y principalmente, mediante estabilizadores dinámicos (Larson & Stern 1986; Terry & Chopp 2000; Jenkins 2009). Esta estabilización dinámica es llevada a cabo principalmente por un conjunto de músculos conocido como el **manguito rotador** (*Figura 18*), también llamado *manguito musculo-tendinoso del hombro* (Hess 2000; Jenkins 2009), cuyos tendones se encuentran fuertemente ligados a la cápsula articular (Terry & Chopp 2000; Jenkins 2009). Anteriormente el manguito está formado por el músculo **subescapular**; posteriormente, por los músculos **supraespinoso**, **infraespinoso** y **redondo menor**.

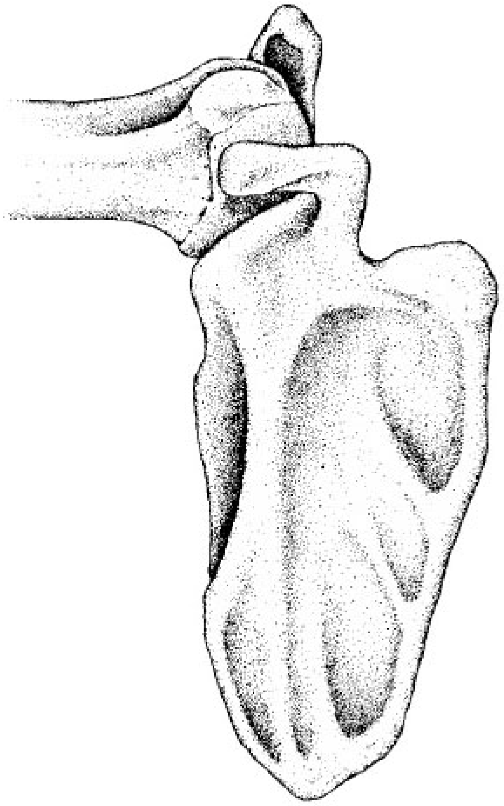

Figura 17. *Articulación glenohumeral en el hombro de* Pan troglodytes *(chimpancé) (adaptada de Larson & Stern 1986).*

Esta disposición de los músculos del manguito rotador proporciona movilidad a la articulación del hombro y permite la estabilización de la articulación (Roberts 1974; Sonnabend & Young 2009) manteniendo la cabeza del húmero en la cavidad glenoidea (Terry & Chopp; Jenkins 2009).

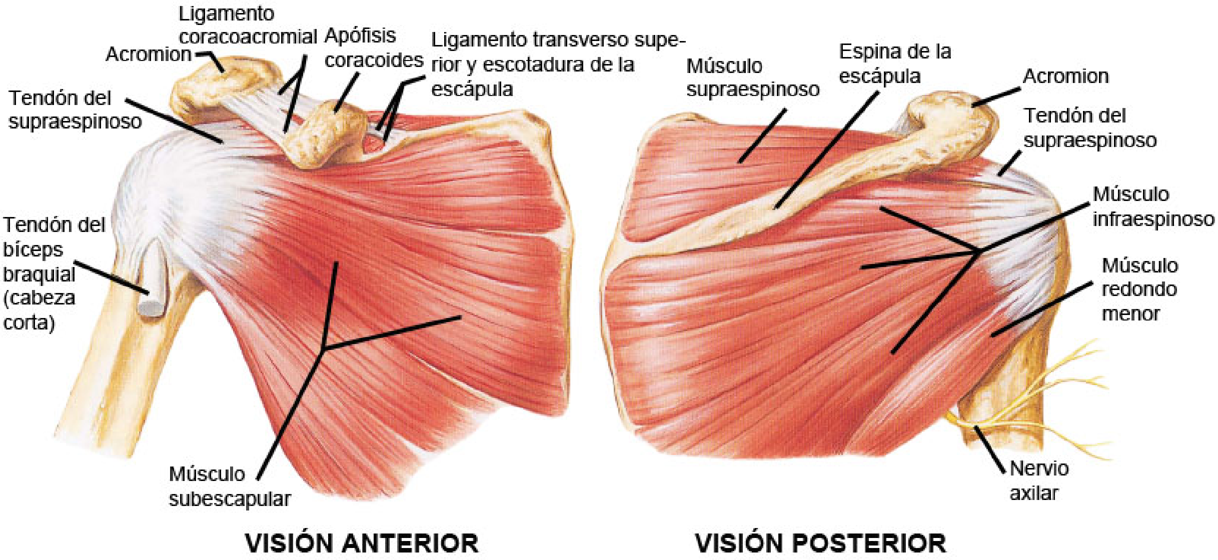

Figura 18. *Vista anterior (izquierda) y posterior (derecha) de los músculos del manguito rotador (adaptada de Netter 2007).*

En relación con el funcionamiento del manguito rotador, durante años se asumió correcto el modelo propuesto por Inman *et al*. (1944). Según este modelo, descrito en humanos modernos (*Homo sapiens*), el manguito rotador funciona como un par de fuerzas actuando a nivel de la articulación glenohumeral. La **unidad superior** estaría formada por los músculos deltoides y supraespinoso, mientras que la **unidad inferior** estaría formada por los músculos infraespinoso, redondo menor y subescapular; en el modelo también se incluye la fricción creada por la cabeza del húmero contra la glenoides. Según Inman *et al*. (1944) el deltoides, ayudado por el supraespinoso, proporciona la fuerza necesaria para elevar la extremidad anterior, mientras que la unidad inferior actúa conjuntamente para retener la cabeza del húmero y evitar la tendencia del deltoides a desplazar la cabeza del húmero superiormente. Este modelo se consideró correcto durante años no sólo en humanos modernos, sino también en grandes simios (Tuttle & Basmajian 1978a,b), asumiendo que la integridad de la articulación glenohumeral se mantiene únicamente mediante estructuras osteoligamentosas (Tuttle & Basmajian 1978a,b). Sin embargo, tras numerosos estudios de electromiografía (EMG) realizados con el fin de entender el funcionamiento de la musculatura del hombro en diferentes especies de primates (Larson & Stern 1986, 1987, 1989, 1992), se ha demostrado que no existe un modelo de pares de fuerzas, sino que cada miembro del manguito rotador tiene un papel funcional distinto y bien definido, tanto en el movimiento como en la estabilización de la articulación glenohumeral (Roberts 1974; Larson & Stern 1986).

2.1.1. Músculo supraespinoso

El músculo supraespinoso es el más estudiado dentro de los músculos del manguito rotador, probablemente debido a su importancia como estabilizador de la articulación, como abductor de la extremidad anterior y debido a sus implicaciones clínicas; en particular el síndrome subacromial, presente únicamente en humanos (Potau *et al*. 2007).

El *músculo supraespinoso* se origina en la cara dorsal de la escápula (*Figura 18*), en la llamada **fosa supraespinosa**, situada por encima de la espina, y también de la fascia que recubre el propio músculo. El músculo pasa por encima de la articulación glenohumeral, insertándose en la cara superior del tubérculo mayor del húmero (Ashton & Oxnard 1963; Jenkins 2009). Antes de insertarse, las fibras del supraespinoso convergen en un tendón corto y denso que se adhiere a la cápsula de la articulación glenohumeral. Entre el músculo supraespinoso y el acromion se encuentra la *bursa subacromial*. Este músculo es principalmente un **abductor** de la extremidad anterior que actúa asistiendo al deltoides en su función elevadora (Larson & Stern 1986, 2013; Aiello & Dean 1990; Jenkins 2009). Además, el supraespinoso tiene una gran importancia oponiendo resistencia al desplazamiento superior del húmero (Larson & Stern 1986, 1987).

2.1.2. Músculo infraespinoso

El músculo infraespinoso se origina en la **fosa infraespinosa** (*Figura 18*) y en la fascia que lo recubre, y se inserta en la cara posterior del tubérculo mayor del húmero, inferiormente a la inserción del supraespinoso. Es un músculo **rotador lateral** del húmero y participa también en el mantenimiento de la posición de la cabeza del húmero durante otros movimientos de la extremidad anterior (Ashton & Oxnard 1963; Larson & Stern 1986, 2013; Aiello & Dean 1990; Jenkins 2009).

2.1.3. Músculo redondo menor

El músculo *redondo menor* (*teres minor*) se origina en los dos tercios superiores de la cara posterior del borde lateral de la escápula (*Figura 18*), y también a partir de un tabique fibroso existente entre este músculo y el infraespinoso por encima y el redondo mayor (*teres major*) por debajo. La inserción tiene lugar en la región inferior de la cara posterior del tubérculo mayor del húmero, directamente por debajo de la inserción del infraespinoso. Al igual que el músculo infraespinoso, el músculo redondo menor es mayoritariamente un **rotador lateral** del húmero y estabilizador de la posición de la cabeza del húmero durante otros movimientos de la extremidad anterior (Ashton & Oxnard 1963; Larson & Stern 1986; Aiello & Dean 1990; Jenkins 2009).

2.1.4. Músculo subescapular

El músculo subescapular se origina en la mayor parte de la cara anterior de la escápula (*Figura 18*), conocida como **fosa subescapular.** Pasa por delante de la articulacion glenohumeral y se inserta en el tubérculo menor del húmero. Antes de la inserción, las fibras convergen en un tendón corto y denso que se adhiere a la cara anterior de la cápsula de la articulación glenohumeral (Ashton & Oxnard 1963). Entre este músculo y la cápsula articular se encuentra la bursa subtendinosa del músculo subescapular, que se abre frecuentemente en la cavidad sinovial de la articulación glenohumeral. El *músculo subescapular* es principalmente un **rotador medial** (Larson 1988; Larson & Stern 1986, 2013), proporcionando además protección para prevenir la luxación anterior de la cabeza de húmero (Aiello & Dean 1990; Jenkins 2009).

2.2. La escápula

2.2.1. Características generales

La **escápula** (*Figura 19*) es un hueso plano que conecta la extremidad anterior con el tórax a través de la clavícula y mediante músculos, de ahí la enorme movilidad de la articulación glenohumeral (Jenkins 2009). Es un hueso triangular con tres bordes (superior, medial o vertebral y lateral o axilar) y dos ángulos (superior e inferior).

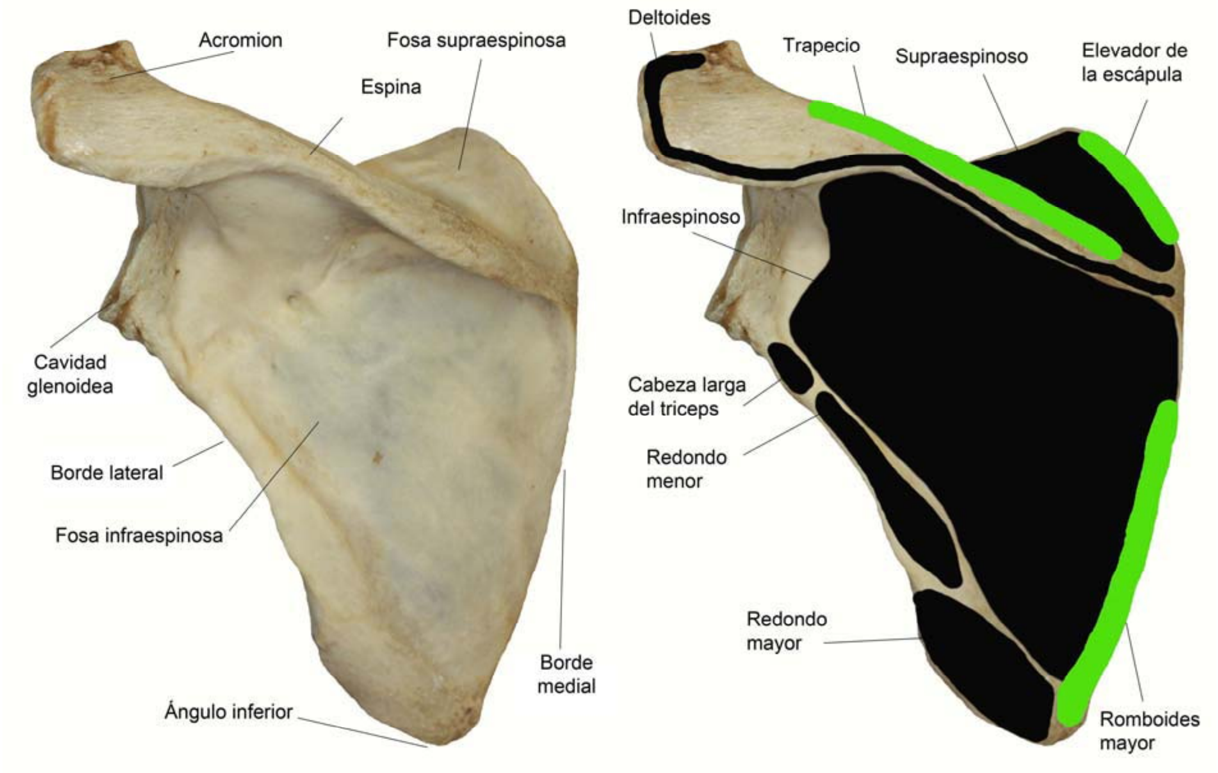

Figura 19. *Características anatómicas de la cara dorsal de la escápula en humanos. A la izquierda se muestran las diferentes partes de la escápula. A la derecha se muestran las áreas de origen (en negro) e inserción (en verde) de los diferentes músculos relacionados con el hombro o con la extremidad anterior (escápula procedente del Servicio de Donación de Cuerpos del Hospital Clinic, Universidad de Barcelona).*

La **cavidad glenoidea** se articula lateralmente con la cabeza del húmero, formando la articulación glenohumeral. Medialmente a la cavidad glenoidea se encuentra el cuello de la escápula. La cara dorsal de la escápula está atravesada por la **espina de la escápula**, que se inicia en el borde medial y se extiende mediolateralmente por encima y más allá de la cavidad glenoidea, formando el **proceso acromial** o **acromion**. La **apófisis coracoides** se proyecta anterosuperiormente sobre la glenoides, sirviendo de inserción a los músculos pectoral menor, cabeza corta del bíceps braquial y coracobraquial (Drake *et al*. 2005). La espina de la escápula divide la cara dorsal de la escápula en dos partes: por encima de la espina se encuentra la **fosa supraespinosa** y por debajo la **fosa infraespinosa**. En el borde lateral de la fosa infraespinosa se encuentra también el origen de los músculos redondo mayor y redondo menor. La cara ventral de la escápula es cóncava y está formada, fundamentalmente, por la **fosa subescapular**.

2.2.2. Morfología vs. *función locomotora*

La **morfología** de la escápula está determinada en gran medida por la **función**, durante la locomoción, de la musculatura de la articulación glenohumeral, de los músculos que mueven y estabilizan el movimiento de la escápula y de los músculos que transmiten el peso corporal hacia las extremidades anteriores (Inman *et al*. 1944; Oxnard 1967, 1977; Roberts 1974; Ashton *et al*. 1976; Larson 1993, 1995; Schmidt & Krause 2011).

Como ya hemos indicado, los músculos que conforman el **manguito rotador** (subescapular, supraespinoso, infraespinoso y redondo menor) juegan un papel fundamental en el *movimiento* y *estabilización* de la articulación glenohumeral en los primates (Inman *et al*. 1944; Wolffson 1950; Ashton & Oxnard 1963; Oxnard 1967, 1968, 1969; Oxnard & Neely 1969; Roberts 1974; Shea 1986; Larson & Stern 1986, 1987, 1989, 1992; Larson *et al*. 1991; Larson 1993, 1995; Potau *et al*. 2009). Diversos estudios empíricos, tanto en músculos en ratas (Wolffson 1950) como en ratones modificados genéticamente (Green *et al*. 2011, 2012), han demostrado claramente que los músculos del manguito rotador tienen una influencia significativa en la forma de la escápula (Howell 1917; Wolffson 1950; Roberts 1974; Green *et al*. 2011, 2012). Esta influencia se refleja en el aumento o reducción del tamaño relativo de los músculos como consecuencia del estrés funcional al que son sometidos, con un gran impacto en la estructura de la escápula (Inman *et al*. 1944; Roberts 1974; Green *et al*. 2011, 2012). Por lo tanto, las adaptaciones de tamaño y forma de los músculos en relación con los requerimientos funcionales de la extremidad anterior pueden provocar cambios en las articulaciones y la posición y orientación de las inserciones musculares (Inman *et al*. 1944; Roberts 1974; Ashton & Oxnard 1964; Oxnard 1967). La estrecha relación entre la forma de la escápula y las características de los músculos del manguito rotador ha sido utilizada para inferir información muscular a partir de información osteológica, mucho más fácil de conseguir debido a las limitaciones (o imposibilidad, como en el caso de especies extintas) relacionadas con el estudio directo de los músculos (básicamente debido a la dificultad de obtener cadáveres de primates). Numerosos estudios han comparado las escápulas de los primates para comprender mejor la relación entre la forma de la escápula y la función locomotora (*Figura 20*) (Frey 1923; Schultz 1930; Inman *et al*. 1944; Ashton & Oxnard 1963, 1964; Ashton *et al*. 1965; Oxnard

1967, 1968, 1969; Oxnard & Neely 1969; Roberts 1974; Corrucini & Ciochon 1976, 1978; Shea 1986; Larson & Stern 1986, 1987, 1989, 1992, 2013; Larson *et al.* 1991; Larson 1993, 1995; Inouye & Shea 1997; Taylor 1997; Inouye & Taylor 2000; Taylor & Slice 2005; Young 2006, 2008; Green *et al*. 2011, 2012).

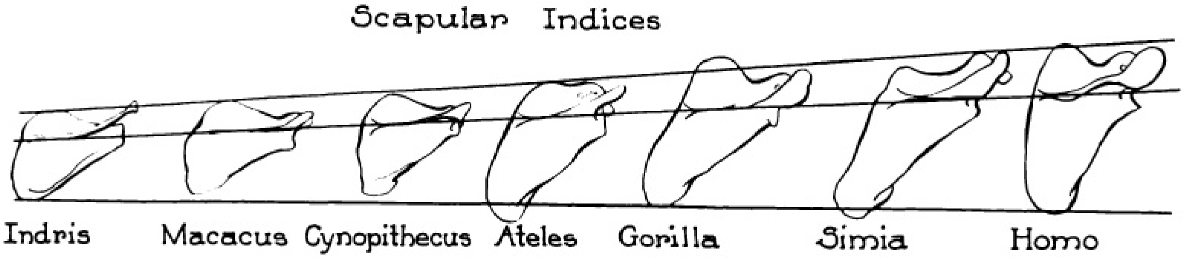

Figura 20. *Estudio osteológico clásico realizado con las escápulas de diferentes especies de primates (adaptada de Inman* et al*. 1944).*

La morfología de la **cara dorsal** de la escápula está especialmente relacionada con las diferencias funcionales en la locomoción de los primates, en particular la forma general de la escápula, la forma y tamaño de las fosas supraespinosa e infraespinosa, la proporción entre estas dos fosas, el área de inserción del músculo redondo mayor y la orientación y longitud de la espina de la escápula (Frey 1923; Schultz 1930; Inman *et al*. 1944; Roberts 1974; Green 2010; Green *et al*. 2012). De todos estos caracteres de la cara dorsal de la escápula, la proporción entre las áreas de las fosas supraespinosa e infraespinosa (S/I) ha sido la más estudiada. Frey (1923) fue el primero en analizar el **spinal fossae index** (SFI), que mide la proporción entre las anchuras de las dos fosas realizada a partir de medidas lineales. El SFI ha sido utilizado en numerosos estudios (Schultz 1930; Inman *et al*. 1944; Roberts 1974; Green 2010) con el fin de relacionar la morfología de la cara dorsal de la escápula con los diferentes comportamientos locomotores en diferentes especies de primates. El análisis comparado del SFI muestra que los hilobátidos presentan los valores más altos para este índice, con valores entre 1 (Schultz 1930) y 2 (Green 2010), comparadas con el resto de primates; los *knuckle-walkers* presentan fosas supraespinosa e infraespinosa de tamaños similares, con valores entre 0,6 (Schultz 1930) y 1 (Green 2010); mientras que los orangutanes, al igual que los humanos, presentan valores muy bajos, en torno a 0,3-0,4 (Schultz 1930; Green 2010), cercanos a los de los primates pronógrados como *Macaca*, con valores entre 0,6 y 0,7 (Green 2010), *Alouatta* y *Ateles*, con valores entre 0.4 y 0,5 (Schultz 1930), o *Papio*, con valores cercanos a 0,3 (Schultz 1930).

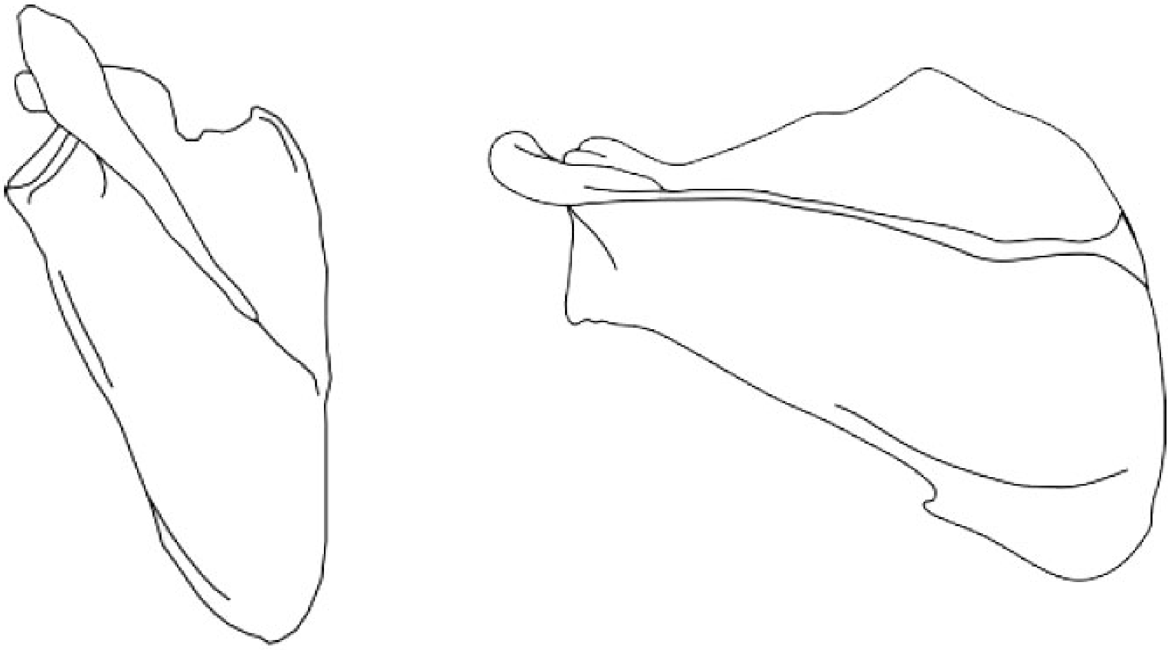

Figura 21. *Escápula típica de un primate suspensor (izquierda) y de un primate cuadrúpedo (derecha) (adaptada de Young 2008).*

Aunque los primates muestran un espectro continuo de formas escapulares, se puede considerar que existe una clara dicotomía entre las formas extremas de este espectro. Por un lado, los

primates cuadrúpedos (tanto arbóreos como terrestres), cuya escápula (*Figura 21*, derecha) se ve principalmente afectada por fuerzas de compresión y se mueve básicamente en un restringido plano parasagital mediante movimientos de retracción-propulsión, tienden a tener escápulas largas (desde el borde medial a la cavidad glenoidea) y estrechas (desde el ángulo superior al ángulo inferior), con la espina perpendicular al borde medial (Schultz 1930; Ashton & Oxnard 1963, 1964; Ashton *et al*. 1965; Roberts 1974; Larson 1993; Young 2008; Schmidt & Krause 2011). En el otro extremo del espectro, los **primates suspensores** (*Figura 21*, izquierda) comparten escápulas cortas y anchas, afectadas principalmente por fuerzas de tensión, con las fosas supraespinosa e infraespinosa grandes y la espina muy inclinada (Schultz 1930; Ashton & Oxnard 1963, 1964; Ashton *et al*. 1965; Roberts 1974; Larson 1993; Young 2008; Schmidt & Krause 2011). Sin embargo, siempre hay que tener en cuenta que la forma de la escápula se ve influenciada en mayor o menor medida por otros factores, como la filogenia, el sustrato por el que se mueven o el peso y tamaño corporal (Roberts 1974; Crompton *et al*. 1987; Charles-Dominique 1990; Larson 1993; Anapol *et al*. 2005; Young 2008; Schmidt & Krause 2011).

3. LA ESCÁPULA Y EL MANGUITO ROTADOR EN PRIMATES

Los análisis osteológicos (Frey 1923; Schultz 1930; Inman *et al*. 1944; Ashton & Oxnard 1963, 1964; Ashton *et al*. 1965; Roberts 1974; Shea 1986; Taylor 1997; Taylor & Slice 2005; Young 2008), electromiográficos (Tuttle & Basmajian 1978a,b; Jungers & Stern 1981; Larson & Stern 1986, 1987, 1989, 1992) y musculares (Potau *et al*. 2009; Green *et al*. 2011, 2012) definen con detalle el papel que juegan los músculos del manguito rotador en el movimiento y la estabilización del hombro en los primates. Generalmente estos estudios se centran en el funcionamiento del manguito rotador en primates hominoideos ortógrados, debido a las implicaciones en evolución humana que tienen, siendo los primates pronógrados menos estudiados en este aspecto. A pesar de ello, muchas de las conclusiones que se derivan de los estudios con primates ortógrados son extrapolables al resto de los primates, ya que la función de los músculos es similar en todas las especies a pesar de las diferencias en el comportamiento locomotor (Larson & Stern 1986, 1987, 1989, 1992).

3.1. El músculo supraespinoso y la fosa supraespinosa

El músculo supraespinoso juega un papel diverso en función del tipo de locomoción:

- En posturas cuadrúpedas y en la fase de soporte de la locomoción cuadrúpeda es un músculo que estabiliza la articulación glenohumeral, impidiendo el desplazamiento del húmero (Larson & Stern 1986, 1987, 1989, 2013).

- Durante la elevación de la extremidad anterior o en movimientos *free arm* (movimientos en los que la extremidad anterior se mueve libremente por encima del nivel de la escápula) juega un papel esencial asistiendo al deltoides durante la abducción de la extremidad anterior (Inman *et al*. 1944; Tuttle & Basmajian 1978a; Larson & Stern 1986, 1989, 2013).
- En la fase inicial de la elevación de la mano es el principal responsable de estabilizar la articulación glenohumeral y prevenir el desplazamiento superior de la cabeza del húmero causada por el deltoides (Howell *et al*. 1986; Larson & Stern 1986, 2013; Thompson *et al*. 1996).

La fosa supraespinosa está relativamente bien desarrollada en primates ortógrados (los hominoideos) en comparación con los primates pronógrados (Frey 1923; Schultz 1930; Inman *et al*. 1944; Roberts 1974; Corruccini & Ciochon 1976; Shea 1986; Larson 1993), igual que el músculo supraespinoso (Potau *et al*. 2009). El gran tamaño de este músculo en primates ortógrados parece estar asociado a la presencia de extremidades anteriores relativamente grandes, pesadas y fuertes, que requieren una enorme estabilización de la articulación glenohumeral durante la elevación (Roberts 1974; Corruccini & Ciochon 1976; Larson & Stern 1986; Larson 1993).

Entre los primates ortógrados, los grandes simios africanos *knuckle-walkers* (gorilas, chimpancés y bonobos) son los que presentan la fosa supraespinosa y el músculo supraespinoso relativamente más grandes (Schultz 1930, Roberts 1974; Aiello & Dean

1990; Potau *et al*. 2007; Young 2008), especialmente en los gorilas, en los que el músculo está hipertrofiado (Schultz 1930; Inman *et al*. 1944; Raven 1950; Roberts 1974). Los gorilas se caracterizan por un enorme tamaño corporal y por el uso de la extremidad anterior en una posición abducida y rotada externamente, dos factores que explican la necesidad de una elevada estabilización de la articulación glenohumeral y, por tanto, de un músculo supraespinoso hipertrofiado (Roberts 1974; Taylor & Slice 2005; Potau *et al*. 2007). Esto se ha comprobado mediante análisis de EMG, que muestran que durante el *knuckle-walking* el músculo supraespinoso, junto con el infraespinoso, es esencial en la estabilización de la articulación glenohumeral, que sufre severas tensiones de cizalla, evitando así la retracción del húmero durante la fase de soporte (Roberts 1974; Tuttle & Basmajian 1978b; Larson & Stern 1987, 1992).

En la primera parte de la fase de balanceo (*swing phase*) durante la elevación de la extremidad anterior, el músculo supraespinoso actúa junto con el deltoides elevando (abducción) la extremidad anterior (Inman *et al*. 1944; Tuttle & Basmajian 1978a; Larson & Stern 1986, 1989). Esta función es especialmente importante en la braquiación, el *vertical climbing* y cualquier tipo de locomoción suspensora (Inman *et al*. 1944; Oxnard 1967; Ashton & Oxnard 1964). Además, a parte de su papel como abductor, el músculo supraespinoso, al insertarse en la cara superior del tubérculo mayor del húmero, es el principal responsable de prevenir el desplazamiento superior de la cabeza del húmero provocada por el deltoides, estabilizando el húmero durante la fase inicial de la elevación de la extremidad (Howell *et al*. 1986; Larson & Stern 1986; Thompson *et al*. 1996). Una vez que la fase inicial de la elevación de la mano termina, la tendencia del deltoides a desplazar el húmero disminuye, por lo que el supraespinoso pasa a asistir al deltoides en la abducción de la extremidad anterior (Larson & Stern 1986).

En los orangutanes, la fosa supraespinosa y el músculo supraespinoso están poco desarrollados en comparación con la fosa y el músculo infraespinosos, siendo la fosa y el músculo supraespinoso más pequeños en comparación con los de los grandes simios africanos (Ashton & Oxnard 1963; Oxnard 1984; Young 2008) pero son ligeramente mayores que los de cualquier primate pronógrado (Ashton & Oxnard 1963; Roberts 1974). Esta fosa supraespinosa pequeña, combinada con la fosa infraespinosa relativamente grande, reflejan un mosaico de características suspensoras y cuadrúpedas. Esto se debe a que el desplazamiento de los orangutanes consiste en una suspensión cautelosa, sin elevar frecuentemente las extremidades anteriores por encima de la cabeza, desplazándose incluso mediante posturas pronógradas (Young 2003; Thorpe & Crompton 2005, 2006).

Los hilobátidos comparten una fosa supraespinosa relativamente grande y, como se verá más adelante una fosa infraespinosa de pequeño tamaño (Schultz 1930; Roberts 1974; Green 2010), que reflejan las enormes especializaciones del hombro para la braquiación (Young 2008).

En los humanos modernos las extremidades anteriores no se utilizan en la locomoción sino que tienen funciones manipulativas, con las manos habitualmente por debajo del nivel del hombro, de forma que se reducen las tensiones de cizalla en la articulación y no es necesario un gran músculo supraespinoso. De este modo, la fosa supraespinosa y el músculo supraespinoso, y en general todo el manguito rotador, se encuentran muy pobremente desarrollados en humanos (Roberts 1974; Potau *et al*. 2007). Esta reducción del manguito rotador permite a la articulación glenohumeral movimientos más rápidos y precisos, esenciales en las habilidades manipulativas de la extremidad anterior humana (Potau *et al*. 2007). Los estudios de EMG en humanos modernos confirman que el supraespinoso actúa conjuntamente con el deltoides para abducir la extremidad anterior (Inman *et al*. 1944). Los humanos muestran una configuración única de los músculos del hombro. Algunas de sus características son similares a las observadas en simios, como un deltoides extremadamente desarrollado, mientras que otras son más parecidas a las de primates cuadrúpedos, como los músculos del manguito rotador poco desarrollados. Este particular mosaico permite a los humanos modernos elevar la mano con total libertad, como en los simios, pero con menor fuerza, duración y frecuencia (Ashton & Oxnard 1963, 1964; Oxnard 1967, 1969; Larson 1993).

En los primates pronógrados cuadrúpedos, como *Chlorocebus aethiops* (Larson & Stern 1989), *Papio anubis* o *Macaca mulatta* (Larson & Stern 1992), el músculo supraespinoso es electromiográficamente activo durante la fase de soporte de la locomoción, estabilizando la articulación glenohumeral (Whitehead & Larson 1994). En los primates pronógrados arbóreos el músculo supraespinoso también puede actuar como elevador de la extremidad anterior asistiendo al deltoides (Larson & Stern 1989, 1992), por lo que la fosa supraespinosa es más grande en los pronógrados cuadrúpedos arbóreos, como *Miopithecus talapoin* o *Colobus*, que en cuadrúpedos terrestres o semiterrestres, como *Papio papio*, *Macaca*, *Chloroce-*

bus aethiops, *Erythrocebus patas* (Roberts 1974), siendo siempre más pequeña que la de los primates ortógrados. Estas diferencias de tamaño de la fosa supraespinosa entre cuadrúpedos arbóreos y terrestres refleja la particular configuración anatómica de la escápula de los primates cuadrúpedos terrestres. Las superficies articulares (cavidad glenoidea y cabeza del húmero) de la articulación glenohumeral de los primates pronógrados cuadrúpedos terrestres permiten un movimiento anteroposterior limitado al plano parasagital (Roberts 1974) y el tubérculo mayor del húmero es grande, lo que estabiliza pasivamente la articulación (Whitehead & Larson 1994) y aumenta el brazo de palanca del supraespinoso. Esta configuración anatómica no precisa un músculo supraespinoso tan grande en estos primates terrestres (Larson 1993; Larson & Stern 1989, 1992).

Si los primates cuadrúpedos arbóreos tuvieran el tubérculo mayor del húmero tan proyectado proximalmente como los terrestres, verían reducida la movilidad de su articulación glenohumeral, necesaria para alcanzar los diferentes sustratos arbóreos. El tubérculo de los primates cuadrúpedos arbóreos es, por este motivo, más reducido y el músculo supraespinoso aumenta de tamaño para compensar la necesidad de estabilización de la articulación (Larson & Stern 1989, 1992).

3.2. El músculo infraespinoso y la fosa infraespinosa

Las principales funciones del músculo infraespinoso en los primates son las siguientes:

- Estabilización de la articulación glenohumeral en posturas cuadrúpedas y durante la fase de soporte de la locomoción cuadrúpeda, junto con el supraespinoso (Larson & Stern 1986, 1987, 1989).

- Estabilización de la articulación glenohumeral durante la fase de soporte del *arm-swinging* (Roberts 1974; Larson & Stern 1986, 2013), resistiendo el estrés transarticular que sufre la articulación mediante una acción depresora de la cabeza del húmero (Roberts 1974; Larson & Stern 1986).
- Además, en movimientos que combinan abducción con rotación lateral (como durante la *swing phase* del *vertical climbing*), el infraespinoso actúa como el principal sinergista del deltoides (Larson & Stern 1986, 2013), un papel que se explica por la orientación superolateral de la cara de inserción del infraespinoso en el tubérculo mayor del húmero, en lugar de la orientación lateral que presentan los primates pronógrados (Larson & Stern 1986; Larson 1995).

Como en el caso de la fosa supraespinosa, los hominoideos predominantemente arbóreos comparten una fosa infraespinosa relativamente grande (Frey 1923; Schultz 1930; Inman *et al*. 1944; Roberts 1974; Corruccini & Ciochon 1976; Manaster 1979; Shea 1986; Larson 1993). Los grandes simios africanos muestran la fosa infraespinosa relativamente más grande, siendo en los gorilas mayor que en los chimpancés, debido a la enorme necesidad de estabilización de la articulación glenohumeral (Schultz 1930; Roberts 1974; Corruccini & Ciochon 1976; Larson 1993), hipótesis confirmada con los estudios de los pesos musculares (Potau *et al*. 2009) y electromiográficos (Tuttle & Basmajian 1978a, b; Larson & Stern 1987). Durante el *knuckle-walking* la articulación glenohumeral soporta el estrés producido por la orientación lateral de la cavidad glenoidea, resultando en una tendencia del húmero a desplazarse dorsalmente (Roberts 1974; Larson & Stern 1987). La estabilización de la articulación se consigue únicamente por la acción de los músculos supraespinoso e infraespinoso, sin la ayuda de los otros músculos del manguito rotador (Tuttle & Basmajian 1978b; Larson & Stern 1987).

La fosa infraespinosa de los orangutanes confirma el importante papel del músculo infraespinoso en la locomoción suspensora. Los orangutanes tienen una fosa infraespinosa grande, aunque menor que la de los grandes simios africanos, por lo que la fosa supraespinosa, a su lado, parece pobremente desarrollada (Roberts 1974). Este gran desarrollo de la fosa infraespinosa está relacionado con el *quadrumanous climbing* de los orangutanes, y con la enorme fuerza muscular necesaria para estabilizar la articulación glenohumeral al elevar la mano por encima de la cabeza (Roberts 1974).

La escápula de los hilobátidos se diferencia de la de los orangutanes en que presenta una fosa infraespinosa relativamente estrecha (Roberts 1974), probablemente relacionada con las especializaciones del hombro requeridas para la braquiación (Roberts 1974; Young 2008).

En los humanos modernos el infraespinoso participa en el control de la posición colgante de la extremidad anterior. Los humanos tienen una fosa infraespinosa relativamente grande, en comparación con la supraespinosa que es relativamente pequeña (Roberts 1974; Aiello & Dean 1990), y una espina prácticamente horizontal (perpendicular al borde vertebral de la escápula), lo que la diferencia del resto de los primates. Esta gran fosa infraespinosa está relacionada con la necesidad de rotación externa de la extremidad anterior durante la elevación de la mano en el plano escapular, retrasando el contacto entre el acromion y el tubérculo mayor del húmero (Inman *et al*. 1944; Basmajian & de Luca 1985).

En la mayoría de primates pronógrados la función del infraespinoso es principalmente la estabilización de la articulación glenohumeral durante la fase de soporte de la locomoción cuadrúpeda y en posturas cuadrúpedas (Whitehead & Larson 1994; Larson & Stern 1989), como sucede también en los grandes simios *knuckle-walkers*. Por otro lado, los primates pronógrados arbóreos también necesitan la estabilización proporcionada por el infraespinoso para elevar las extremidades anteriores al desplazarse por el dosel arbóreo discontinuo (Whitehead & Larson 1994; Larson 1995).

3.3. El músculo redondo menor y la fosa del redondo menor

El **redondo menor** es un músculo ausente en mamíferos filogenéticamente generalizados que se origina a partir del músculo deltoides (Inman *et al*. 1944; De Palma 2008). A medida que la fosa infraespinosa fue aumentando su tamaño progresivamente, un fragmento del deltoides se separó y aumentó de tamaño también. Progresivamente, los cambios esqueléticos alteraron la posición de este "nuevo" músculo, permitiéndole actuar sobre el húmero hacia abajo (Inman *et al*. 1944; De Palma 2008). Según Ashton & Oxnard (1963), en primates hominoideos este músculo está completamente diferenciado del deltoides y del infraespinoso, mientras que en el resto de primates su presencia es variable.

Aunque durante mucho tiempo se pensó que el redondo menor formaba un grupo funcional con los músculos subescapular e infraespinoso, presionando la cabeza del húmero hacia abajo y rotándolo (Inman *et al*. 1944; Tuttle & Basmajian 1978a,b) actualmente se considera que el redondo menor es fundamentalmente un rotador lateral del húmero, participando en el mantenimiento de la posición de la cabeza del húmero en la cavidad glenoidea (Larson & Stern 1986; Aiello & Dean 1990; Jenkins 2009).

Es importante resaltar que el redondo menor, y una gran parte del subescapular, como veremos luego, no está involucrado en la *swing phase* de la elevación de la mano (Larson & Stern 1986), estando activo solamente durante su fase de soporte. Esto parece indicar que, al menos en comportamientos que requieren la elevación de la mano, el redondo menor ayuda a resistir el estrés de tensión transarticular de la articulación glenohumeral (Larson & Stern 1986) y actúa como retractor del húmero durante el *hoisting* en orangutanes (Tuttle & Basmajian 1978a). Es decir, el redondo menor es un músculo aductor de la extremidad anterior (Larson & Stern 1986). Durante el *knuckle-walking* actúa, al menos en los chimpancés, en la rotación lateral de la articulación glenohumeral (Larson & Stern 1987).

3.4. El músculo subescapular y la fosa subescapular

El músculo subescapular presenta una diferenciación funcional relacionada con la orientación de las fibras musculares y de origen a partir de diversas regiones de la fosa subescapular (Larson & Stern 1986). En el caso mejor estudiado por Larson & Stern (1986, 1987), el chimpancé, se distinguen tres partes diferenciadas (*Figura 22*): una porción superior que se origina en la región superior de la fosa subescapular, aproximadamente a nivel de la fosa supraespinosa; una porción media que se origina en la cara anterior aproximadamente a nivel de la fosa infraespinosa; y una porción inferior que se origina en el surco ventral, lateral a la barra axilar, y a partir de la fascia compartida con el músculo redondo mayor (Larson & Stern 1986). Cada región del músculo subescapular actúa individualmente en función de la posición de la extremidad anterior(Larson & Stern 1986; Larson 1988). Existe, además, una clara relación entre la región de la cara del tubérculo menor del húmero, donde se insertan las fibras, y la función de las fibras musculares (Larson 1995). La abducción y rotación medial las realizan aquellas fibras que se insertan en la región proximal, correspondientes a la porción superior del subescapular, mientras que la aducción y rotación medial las realizan fibras que se insertan distalmente, correspondientes a la porción inferior del subescapular (Larson & Stern 1986; Larson 1988, 1995).

El músculo subescapular es principalmente un rotador medial de la extremidad anterior; rotación que puede combinarse con abducción (por la porción superior) o aducción (por la porción inferior) dependiendo de la posición y los movimientos de la extremidad (Larson & Stern 1986; Larson 1988). La rotación medial del húmero es especialmente importante durante el *knuckle-walking* de los grandes simios africanos, contribuyendo a la estabilización de la articulación glenohumeral (Tuttle & Basmajian 1978b; Larson & Stern 1987).

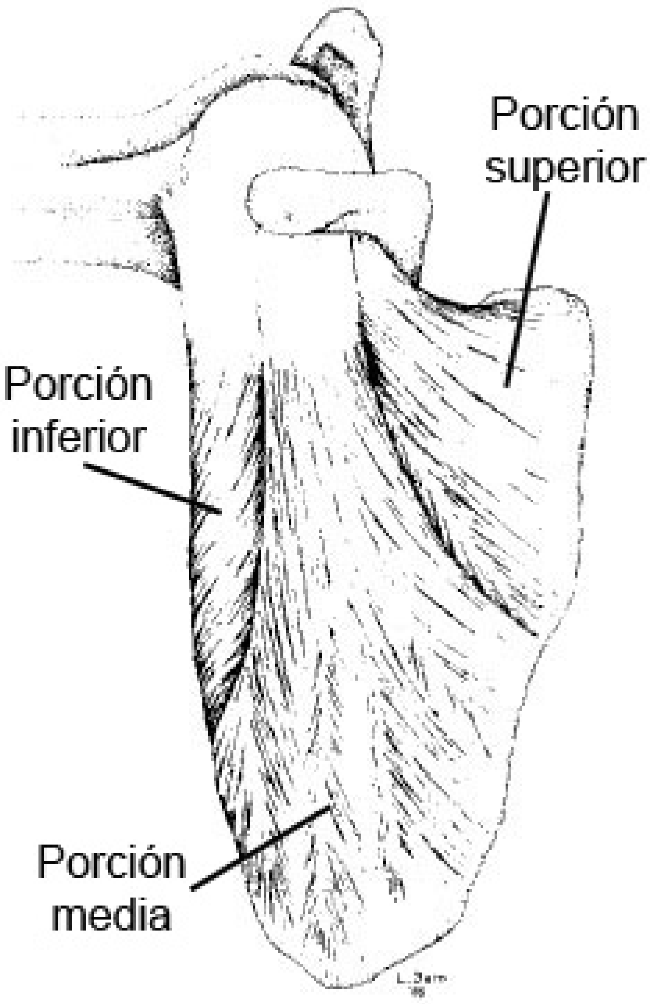

Figura 22. *Músculo subescapular de* Pan troglodytes *(chimpancé) en el que se observan las tres partes (superior, media e inferior) del músculo (adaptada de Larson 1988).*

Esta estabilización tiene lugar compensando las fuerzas de cizalla que soporta la articulación debido a la posición dorsal de la escápula (Roberts 1974; Larson 1993). Este papel del subescapular es consistente con los resultados obtenidos a partir de estudios de EMG (Tuttle & Basmajian 1978b; Larson & Stern 1987) y con el peso muscular relativamente grande de este músculo en chimpancés (Inman *et al*. 1944; Potau *et al*. 2009).

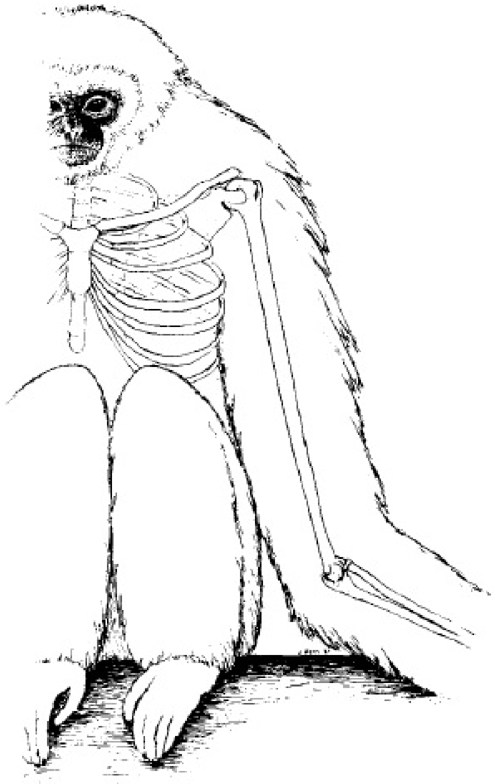

Figura 23. *Cintura escapular de un hilobátido en el que la torsión de la cabeza del húmero es escasa, por lo que este grupo requiere un gran músculo subescapular para realizar la rotación medial necesaria durante la fase de soporte del* vertical climbing *(adaptada de Larson 1988).*

Durante la fase de soporte del *arm-swinging*, al menos en chimpancés, el músculo subescapular no contribuye a la estabilización de la articulación (Larson & Stern 1986; Larson 1988), lo que confirma que el modelo de funcionamiento del manguito rotador descrito por Inman *et al*. (1944) y apoyado por Tuttle & Basmajian (1978a,b) es erróneo (véase apartado I.2.1). Por el contrario, este músculo actúa durante la fase de soporte del *arm-swinging* en hilobátidos (Jungers & Stern 1984), lo que se asocia a una función rotadora más que estabilizadora, ya que los hilobátidos realizan más movimientos *free arm* que los chimpancés (Larson 1988; Larson & Stern 2013). En hilobátidos el papel más importante del músculo subescapular tiene lugar en la fase de soporte (o *pull-up phase*) del *vertical climbing*, en la que su papel como rotador medial es crucial debido a la escasa torsión humeral que presentan (*Figura 23*) (Larson & Stern 1986, 2013; Larson 1988).

4. ESTRUCTURA DE LA TESIS

Esta Tesis Doctoral está estructurada como un *conjunto de seis publicaciones* que analizan aspectos funcionales y adaptativos de la escápula desde una perspectiva anatómica. En esta sección se describen brevemente los trabajos realizados y las técnicas de análisis utilizadas en cada estudio.

4.1. Descripción anatómica

En el apartado 1 del capítulo V (Bello-Hellegouarch *et al*. 2012) presentamos una revisión bibliográfica que fue publicada en formato de capítulo de libro (*Nova Science Publishers*). En ella se describe la morfología escapular y los aspectos funcionales y anatómicos de los músculos del manguito rotador en primates hominoideos, con especial incidencia en las transformaciones y adaptaciones evolutivas relacionadas con los diferentes tipos de locomoción que realizan los hilobátidos, orangutanes, gorilas, chimpancés y humanos modernos.

4.2. Análisis morfológico

4.2.1. Morfometría geométrica

Los análisis de morfometría geométrica (GM) se basan en la configuración espacial de *landmarks*, que son puntos homólogos que pueden localizarse de modo preciso en cada uno de los especímenes estudiados. La GM se centra en caracterizar la forma de las estructuras cuantificando su variación morfológica (Bookstein 1991; Zelditch *et al*. 2004). En GM, la forma de un objeto incluye todas sus características geométricas, excepto las relacionadas con su tamaño, posición y orientación, lo que se consigue mediante un procedimiento conocido como *procrustes superimposition* (*Figura 24*). Para extraer la información geométrica, se re-escalan las configuraciones de *landmarks* a un tamaño estándar, se desplazan todas a una posición estándar y se rotan a una orientación también estándar. Las coordenadas de los *landmarks* obtenidas tras esta superimposición, conocidas como *procrustes coordinates*, representan la variación de formas del conjunto de estructuras que se comparan en los subsiguientes análisis estadísticos.

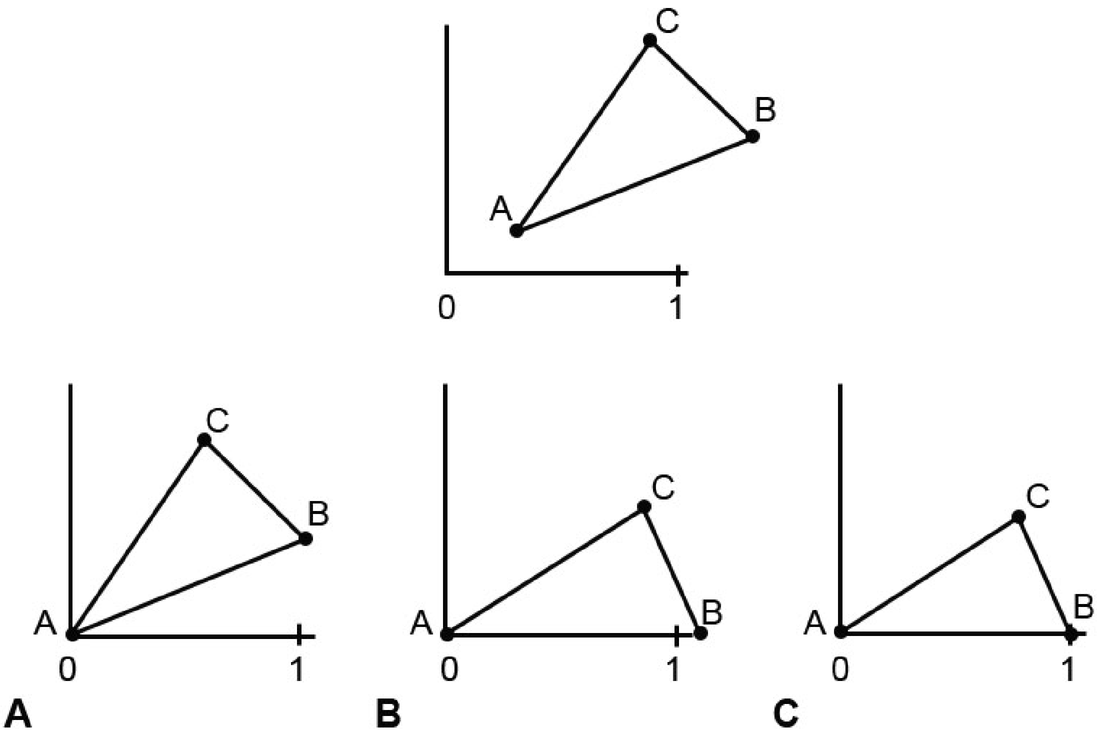

Figura 24. *Tres transformaciones geométricas que no alteran la forma de un objeto (en este caso, un triángulo): (A) traslación (se elimina la información de posición); (B) rotación (se elimina la información de orientación); (C) reescalado (se elimina la información de tamaño) (adaptada de Zelditch* et al. *2004).*

En las secciones de materiales y métodos de los apartados 2, 3 y 4 del capítulo V (Publicaciones) se describen con detalle la metodología morfo-geométrica utilizada.

a. Primates ortógrados

Taylor & Slice (2005) analizaron mediante morfometría geométrica en dos dimensiones la forma de la cara dorsal de la escápula de chimpancés y gorilas, incluyendo las fosas supraespinosa e infraespinosa, la espina y el acromion. Encontraron diferencias tanto entre chimpancés y gorilas, como entre las dos especies de gorilas analizadas (*Gorilla beringei* y *Gorilla gorilla*), pero no encontraron un patrón funcional claro entre la forma de la escápula y la locomoción, siendo consistente con estudios previos, más convencionales (análisis de medidas lineales de la escápula), de la morfología de la escápula en grandes simios africanos (Shea 1986; Inouye & Shea 1997; Taylor 1997; Inouye & Taylor 2000). Estos resultados sugirieron que las diferencias en la forma de la escápula de los hominoideos podrían ser demasiado sutiles para reflejar con precisión las diferencias observadas en su comportamiento locomotor (Ward 1997). Sin embargo, Young (2008) empleó la GM en tres dimensiones para comparar los cambios ontogenéticos de la escápula de diferentes primates antropoideos, encontrando que el principal factor que la determina es su función, de modo que existe una convergencia en la forma de la escápula en especies con modos de locomoción similares. No obstante, Young (2006, 2008) nunca incluyó escápulas humanas al analizar la variación de la forma de la escápula, tanto a nivel intra- como inter-específico.

A pesar de los numerosos estudios realizados sobre la forma de la escápula, algunos autores consideran que todavía no se ha encontrado una interdependencia entre las proporciones de las fosas escapulares y los comportamientos locomotores (Shea 1986; Inouye & Shea 1997; Taylor 1997; Ward 1997; Inouye & Taylor 2000; Taylor & Slice 2005). Otros, en cambio, sugieren una clara asociación entre la forma de la escápula y la función locomotora (Schultz 1930; Roberts 1974; Young 2006, 2008). En el apartado 2 del capítulo V intentamos clarificar la relación entre la proporción de las fosas supraespinosa e infraespinosa y los comportamientos locomotores en hominoideos mediante un análisis de GM en dos dimensiones de la cara dorsal de la escápula de primates hominoideos, incluyendo al humano moderno.

b. Cautividad *vs*. libertad

La mayoría de las colecciones osteológicas procedentes de museos provienen de animales que vivieron en cautividad. Muchos autores descartan el uso de estas colecciones en estudios sobre las adaptaciones anatómicas y morfológicas de los huesos (O'Regan 2001; O'Regan & Kitchener 2005). Se asume que las restricciones relacionadas con el espacio limitado de los recintos en los que vivieron y las condiciones no naturales propias de una vida en cautividad podrían tener un efecto significativo en sus comportamientos posturales y locomotores, de modo que los datos obtenidos a partir de individuos en cautividad no serían informativos sobre la morfología del hueso y las adaptaciones anatómicas de los animales que viven en libertad. Sin embargo, nunca se ha estudiado esta posible influencia de las condiciones de cautividad sobre de la escápula de primates. Por ello, en el apartado 3 del capítulo V realizamos un estudio de GM en dos dimensiones de la cara dorsal de la escápula (cuya morfología, como se muestra en el apartado 2 del capítulo V, está altamente relacionada con los tipos de locomoción) de grandes simios procedentes tanto de libertad como de cautividad, con el fin de clarificar el efecto que las condiciones de cautividad tienen sobre la morfología de la escápula.

c. Primates pronógrados

En el apartado 4 del capítulo V estudiamos la relación entre los patrones locomotores de los primates pronógrados (incluyendo diferentes especies de estrepsirrinos y haplorrinos) y la morfología del lado dorsal de la escápula. Nuestro objetivo es asociar cada categoría locomotora con una forma escapular específica, con el fin de mejorar la comprensión de los requerimientos anatómicos de cada modo particular de locomoción. Con este objetivo realizamos un análisis de GM en dos dimensiones del lado dorsal de la escápula de numerosas especies de primates pronógrados con diferentes patrones locomotores. Se analizan las regresiones multivariadas de las formas escapulares para cada tipo de locomoción para conocer su influencia en la forma de la escápula y extraer la forma asociada a cada categoría locomotora. Además, se analiza la influencia de diversos factores biológicos y ecológicos que se han demostrado influyentes en la morfología de los huesos de la extremidad anterior, como son la filogenia, el peso corporal, el tamaño de la escápula o las preferencias de altura del dosel arbóreo (Roberts 1974; Crompton *et al*. 1987; Charles-Dominique 1990; Larson 1993; Anapol *et al*. 2005; Young 2008; Schmidt & Krause 2011).

4.2.2. Análisis cuantitativo de las fosas supraespinosa e infraespinosa

En el apartado 2 del capítulo V comparamos diferentes metodologías de análisis de la proporción entre las fosas supraespinosa e infraespinosa. Nuestro objetivo es conocer, por un lado, cuál de las medidas es más efectiva para discriminar la muestra por grupos locomotores y, por otro, determinar cuál permite estimar mejor los pesos de los músculos supraespinoso e infraespinoso (conjuntamente con el músculo redondo menor), y conocer así si existe una relación directa entre el tamaño de los músculos y el de sus áreas de inserción. Para ello calculamos la proporción entre las fosas supraespinosa e infraespinosa mediante tres metodologías distintas:

- *Spinal fossae index* (SFI): medida empleada en estudios clásicos de la cara dorsal de la escápula (Frey 1923; Schultz 1930; Inman *et al*. 1944; Roberts 1974), consiste en la relación entre la anchura (medida lineal) de la fosa supraespinosa y la anchura de la fosa infraespinosa.
- Índice de las áreas en 2D (2DI): la proporción entre las áreas en 2D de la fosa supraespinosa y la fosa infraespinosa; estas áreas se obtuvieron a partir de fotografías de las escápulas.
- Índice de las áreas en 3D (3DI): la relación entre las áreas en 3D de la fosa supraespinosa y la fosa infraespinosa; se obtuvieron mediante escaneado en 3D de moldes de las fosas de la cara dorsal de la escápula.

Estas medidas se compararon con la proporción obtenida entre los pesos musculares del supraespinoso e infraespinoso (incluido el redondo menor).

4.3. Análisis molecular

Las características fisiológicas de los músculos, como la velocidad de contracción, la fuerza y la resistencia a la fatiga, dependen en gran medida de la expresión diferencial de las diferentes isoformas de la cadena pesada de la miosina (MHC) presentes en las fibras musculares (Botinelli & Reggiani 2000). Los músculos esqueléticos de mamíferos adultos expresan tres tipos de isoformas de MHC en diferentes proporciones: la MHC-I (lenta), la MHC-IIa (rápida), y la MHC-IIx (más rápida). Una cuarta isoforma, la MHC-IIb, se expresa solamente en músculos de mamíferos muy pequeños (Baldwin & Haddad 2001). La isoforma MHC-I se expresa principalmente en fibras de contracción lenta; la isoforma MHC-IIa en fibras de contracción rápida; y la isoforma MHC-IIx en fibras rápidas glucolíticas. Las fibras de tipo IIx son más fuertes, rápidas, y menos resistentes a la fatiga que las fibras de tipo IIa, mientras que las de tipo I son las menos fuertes y rápidas, pero las más resistentes a la fatiga (Botinelli *et al*. 1999; Pette & Staron 2000). En general, los músculos posturales lentos expresan principalmente la isoforma MHC-I, con una expresión variable de la isoforma MHC-IIa (Fitts *et al*. 1991; Baldwin 1996; Fitts & Widrick 1996; Schiaffino & Reggiani 1996; Rivero *et al*. 1999; Talmadge 2000). Por el contrario, los músculos más potentes, rápidos, pero menos resistentes a la fatiga expresan las tres isoformas en proporciones variables, aunque generalmente la expresión de la isoforma MHC-II es más elevada (Larsson & Moss 1993; Harridge *et al.* 1998).

Aunque existe abundante información en la literatura sobre la anatomía y la estructura del músculo supraespinoso en diferentes especies de primates, hasta el momento pocos estudios han examinado las características moleculares de este músculo. La mayoría de ellos se basan en pocas especies y analizan la cantidad y distribución de los diferentes tipos de fibras en el músculo mediante tinciones ATPasa (Schmidt & Schilling 2007; Singh *et al*. 2002), pero ninguno examina la expresión del mRNA de las diferentes isoformas de MHC en el músculo supraespinoso. El empleo de una RT-PCR (*real-time polymerase chain reaction*) para analizar las isoformas de MHC puede proporcionar nueva información sobre las características moleculares del músculo supraespinoso en diferentes especies de primates y su relación con los tipos de locomoción. La RT-PCR tiene ventajas frente a la tinción ATPasa, que se emplea únicamente en músculos obtenidos a partir de biopsias o inmediatamente después de morir, ya que la variación del pH *post-mortem* puede alterar los resultados. La RT-PCR puede aplicarse a músculos obtenidos a partir de cadáveres criopreservados.

4.3.1. Primates con diferentes tipos de locomoción

En el apartado 5 del capítulo V cuantificamos la expresión de mRNA de las tres isoformas del MHC empleando RT-PCR en músculos supraespinosos de humanos modernos y 12 especies de primates. El principal objetivo es obtener información de las características funcionales del músculo supraespinoso y asociarlas con adaptaciones a los tipos de locomoción de las especies estudiadas. Nuestra hipótesis consiste en que el patrón de expresión diferencial de las isoformas de MHC está relacionado con las diferentes funciones del músculo supraespinoso en primates ortógrados y pronógrados.

4.3.2. Humanos con diferentes edades y sexos

En el apartado 6 del capítulo V cuantificamos la expresión del mRNA de las tres isoformas de MHC en músculos supraespinosos de humanos modernos para determinar si su expresión es similar a la de un músculo postural (con mayor expresión de la MHC-I lenta, apropiada para su función como estabilizador de la articulación glenohumeral) o más parecida a la de un músculo fásico (con una mayor expresión de la isoforma MHC-II rápida, adecuada para su papel en la elevación de la extremidad anterior). Por otra parte, el análisis de la expresión de las isoformas de MHC en el músculo supraespinoso, en función de la edad y el sexo, podría contribuir a la comprensión de los mecanismos etiopatogénicos potenciales del síndrome subacromial, relacionados con el debilitamiento de los músculos del manguito rotador.

5. OBJETIVOS

El estudio de las adaptaciones de la locomoción en primates se han centrado fundamentalmente en la cintura pélvica y la extremidades posteriores, no sólo debido al interés asociado con la aparición del bipedismo y del origen y evolución de nuestra propia especie, sino también debido a la idea generalizada de que la cintura escapular y la extremidad anterior presentan escasas diferencias entre los patrones locomotores. Sin embargo, en la Introducción hemos podido constatar que la morfología de esta región anatómica, mucho menos estudiada que la cintura pélvica, está estrechamente relacionada con los diferentes comportamientos locomotores observados en el orden de los Primates.

El objetivo principal de esta Tesis Doctoral es conocer mejor la diversidad anatómica de la escápula y los músculos del manguito rotador en el orden de los Primates, integrando diferentes enfoques metodológicos para caracterizar las adaptaciones anatómicas y funcionales de esta región. Esta Tesis Doctoral se centra principalmente en la cara dorsal de la escápula y en los músculos que se insertan en ella. Este objetivo general se puede concretar en seis objetivos concretos:

1. Clarificar si existe alguna relación entre la proporción de las fosas supraespinosa e infraespinosa y los comportamientos locomotores de los primates hominoideos, incluyendo humanos modernos, con el fin de terminar con la controversia acerca de si las diferencias morfológicas entre las escápulas de primates hominoideos se asocian con un patrón funcional o no.

2. Analizar la proporción entre las fosas supraespinosa e infraespinosa (índice S/I) en las escápulas de primates hominoideos, no sólo cualitativamente, mediante morfometría geométrica, sino cuantitativamente, mediante mediciones de las áreas de inserción de los músculos dorsales del manguito rotador.
3. Comparar las diferentes metodologías utilizadas para cuantificar el índice S/I con el peso real de los músculos que se insertan en estas fosas, con el fin de conocer su correlación con el peso muscular real y su utilidad como indicador adaptativo fiable en caso de ausencia de musculatura, situación frecuente en colecciones osteológicas o en el caso de escápulas fósiles.
4. Evaluar si las condiciones en cautividad influyen de manera significativa en la morfología de la escápula de los primates, y comprobar si las escápulas obtenidas a partir de primates en cautividad se pueden utilizar con confianza en estudios anatómicos y funcionales.
5. Hacer un estudio detallado de las adaptaciones anatómicas y funcionales de la cara dorsal de la escápula para cada uno de los primates pronógrados y sus tipos de locomoción.
6. Comprobar si la expresión diferencial de las isoformas de la miosina del músculo supraespinoso sigue un patrón funcional relacionado con los modos de locomoción en primates, incluyendo humanos modernos, y, por tanto, con su función en cada tipo de locomoción.

6. INFORME DE LOS DIRECTORES

La doctoranda, Gaëlle Bello Hellegouarch, presenta su Tesis Doctoral siguiendo el formato de compendio de publicaciones establecido por la Universitat de Barcelona. Desde un principio su investigación se centró en el estudio de las adaptaciones anatómicas y funcionales de la escápula y los músculos del manguito rotador a los tipos de locomoción presentes en el orden de los Primates. Un objetivo primordial de esta investigación fue determinar si existen diferencias morfológicas en las escápulas relacionadas con los tipos de locomoción y la función diferencial de los músculos del manguito rotador. También se fijó como objetivo caracterizar la utilidad del análisis de las isoformas de las miosinas de los músculos del manguito rotador para comparar grupos locomotores. Durante el desarrollo de la investigación se demostró que era necesario analizar la influencia de las condiciones de la vida en cautividad sobre la morfología de la escápula, para determinar si las colecciones osteológicas procedentes de individuos en cautividad son representativas del grupo estudiado.

Esta Tesis Doctoral ha generado seis publicaciones científicas: un capítulo de libro internacional (revisado por evaluadores externos y publicado por *Nova Science Publishers*) y cinco artículos en revistas internacionales referenciadas en el *Science Citation Index*. De estos, cuatro ya están aceptados y publicados y uno se está terminando para ser evaluado. La doctoranda consta como primera autora en cuatro de las publicaciones, como tercera autora en una y como quinta autora en otra.

Además de las seis publicaciones incluidas en su Tesis Doctoral, la doctoranda es autora en otras ocho publicaciones, fruto de sus estancias y colaboraciones internacionales, no incluidas en esta Tesis Doctoral por no estar directamente relacionadas con el tema estudiado. De esas, cuatro son atlas de anatomía publicados por Science Publishers y por Taylor & Francis, y las restantes son artículos publicados en revistas internacionales referenciadas en el *Science Citation Index*, todos ellos ya aceptados y publicados. La doctoranda consta como primera autora en una de estas ocho publicaciones (véase más abajo).

A continuación se presentan las publicaciones que forman parte de la presente Tesis Doctoral, citadas en orden cronológico de aparición, indicando los autores, año, título, referencia y posición e impacto de la revista en que se ha publicado. Para cada una se describe la labor concreta realizada exclusivamente por la doctoranda, Gaëlle Bello Hellegouarch.

Publicaciones que forman parte de la presente Tesis Doctoral

1. Potau JM, Artells R, **Bello G**, Muñoz C, Monzó M, Pastor JF, de Paz F, Barbosa M, Diogo R, Wood B (2011) Expression of myosin heavy chain isoforms in the supraspinatus muscle of different primate species: implications for the study of the adaptation of primate shoulder muscles to different locomotor modes. *International Journal of Primatology* **32 (4)**: 931-944.

   IF = 1,786 (2012); 38/151 Q2 [ZOOLOGY]

En este trabajo se analiza la utilidad del estudio de la expresión de las isoformas de la cadena pesada de las miosinas en la caracterización de las adaptaciones a la locomoción observadas en los músculos del manguito rotador en primates. La doctoranda colaboró en la disección de los primates analizados y en el procesamiento y posterior análisis molecular de la musculatura estudiada.

2. **Bello-Hellegouarch G**, Potau JM, Arias-Martorell J, Pastor JF, Diogo R, Pérez-Pérez A (2012) *The rotator cuff muscles in Hominoidea: evolution and adaptations to different types of locomotion.* In: Primates: classification, evolution and behavior. Hughes EF, Hill ME (Eds.). Nova Science Publishers (Hauppauge, US).

Este capítulo de un libro presenta una revisión anatómica y funcional de los músculos del manguito rotador y de la escápula en los primates hominoideos, centrándonos en el funcionamiento e importancia de cada músculo en sus diferentes modos de locomoción. La doctoranda, como primera autora, realizó la revisión bibliográfica, redactó el borrador del capítulo e incorporó las aportaciones de los demás autores.

3. Potau JM, Artells R, Muñoz C, Díaz T, **Bello-Hellegouarch G**, Arias-Martorell J, Pérez-Pérez A, Monzó M (2012) Expression of myosin heavy chain isoforms in the human supraspinatus muscle. Variations related to age and sex. *Cells Tissues Organs* **196 (5)**: 456-462.

IF = 1,961 (2012); 6/21 Q2 [ANATOMY & MORPHOLOGY]

Este estudio analiza la expresión diferencial de las isoformas de la cadena pesada de las miosinas del músculo supraespinoso de humanos. La doctoranda colaboró en la disección de los cadáveres analizados y en el procesamiento y posterior análisis molecular de la muestra estudiada.

4. **Bello-Hellegouarch G**, Potau JM, Arias-Martorell J, Pastor JF, Pérez-Pérez A (2013) A Comparison of Qualitative and Quantitative Methodological Approaches to Characterizing the Dorsal Side of the Scapula in Hominoidea and Its Relationship to Locomotion. *International Journal of Primatology* **34**: 315-336.

   IF = 1,786 (2012); 38/151 Q2 [ZOOLOGY]

Este trabajo constituye una de las principales aportaciones de la Tesis Doctoral de la doctoranda Gaëlle Bello Hellegouarch. En él se comparan, mediante morfometría geométrica en dos dimensiones las escápulas de los primates hominoideos, incluidos los humanos, con el fin de determinar sus adaptaciones específicas a cada modo de locomoción. Se comparan diferentes metodologías de análisis de la relación entre la fosa supraespinosa y la infraespinosa para caracterizar cuál de ellas estima mejor el desarrollo de la musculatura. La doctoranda realizó la toma de muestra, los moldes de las fosas, el escaneado y su posterior análisis estadístico y la redacción del trabajo.

5. **Bello-Hellegouarch G**, Potau JM, Arias-Martorell J, Pastor JF, Pérez-Pérez A (2013) Brief communication: Morphological effects of captivity. A geometric morphometric analysis of the dorsal side of the scapula in captive-bred and wild-caught

Hominidae. *American Journal of Physical Anthropology* **152**: 306-310.

IF = 2,481 (2012); 7/83 Q1 [ANTHROPOLOGY]

Esta publicación se realizó con el fin de comparar materiales osteológicos procedentes de animales en cautividad y libertad. No es infrecuente que los revisores de las revistas destaquen las limitaciones del uso de animales cautivos considerando que no son representativos de la especie en su conjunto ni fiables para deducir comportamientos en libertad. Este trabajo sugiere que, al menos en el caso de la escápula, las colecciones osteológicas son útiles y fiables en estudios morfológicos. La doctoranda realizó la toma de muestra, las fotografías, los análisis estadísticos y la redacción del borrador del trabajo.

6. **Bello-Hellegouarch G**, Potau JM, Arias-Martorell J, Pastor JF, Pérez-Pérez A (en revisión) Two-dimensional geometric morphometric analysis of the anatomical adaptations to locomotor behaviors of pronograde primates in the dorsal side of the scapula.

Esta publicación completa los resultados que se derivan de la Tesis Doctoral de la doctoranda Gaëlle Bello Hellegouarch. En ella se analizan las adaptaciones anatómicas de la cara dorsal de la escápula asociadas a los modos de locomoción en primates pronógrados. Tanto la obtención de muestra, como el análisis y la redacción del borrador de este trabajo fueron realizados por la doctoranda.

Otras publicaciones que no forman parte de la presente Tesis Doctoral

Aunque no forman parte de la presente Tesis Doctoral, se derivan de las labores científicas desarrolladas durante la misma y de las colaboraciones realizadas con diversos grupos de investigación nacionales e internacionales.

1. Aversi-Ferreira TA, Diogo R, Potau JM, **Bello G**, Pastor JF, Ashraf Aziz M (2010) Comparative anatomical study of the forearm extensor muscles of Cebus libidinosus (Rylands *et al*., 2000; Primates, Cebidae), modern humans, and other Primates, with comments on Primate evolution, phylogeny, and manipulatory behavior. *The Anatomical Record* **293**: 2056-2070. IF = 1,343.

2. Diogo R, Potau JM, Pastor JF, de Paz FJ, Ferrero EM, **Bello G**, Barbosa M, Wood BA (2010) Photographic and descriptive musculoeskeletal atlas of Gorilla: With notes on the attachments, variations, innervations, synonymy and weight of the muscles. Science Publishers (Enfield, USA).

3. Diogo R, Potau JM, Pastor JF, de Paz F, Barbosa MM, Ferrero EM, **Bello G**, Aziz MA, Burrows A, Arias-Martorell J & Wood BA (2012) Photographic and descriptive atlas of gibbons and siamangs (Hylobates) - with notes on the attachments, variations, innervation, synonymy and weight of the muscles. Taylor & Francis (Oxford, UK).

4. Arias-Martorell J, Potau JM, **Bello-Hellegouarch G**, Pastor JF, Pérez-Pérez A (2012) 3D geometric morphometric analysis of the proximal epiphysis of the hominoid humerus. Journal of Anatomy **221** (5): 394-405. IF = 2,357.

5. **Bello-Hellegouarch G**, Aziz MA, Ferrero EM, Kern M, Francis N, Diogo R (2012) "Pollical palmar interosseous muscle" (Musculus adductor pollicis accessorius): Attachments, innervation, variations, phylogeny, and implications for human evolution and medicine. Journal of Morphology **274** (3): 275-293. IF = 1,719.

6. Diogo R, Pastor F, de Paz F, Potau JM, **Bello-Hellegouarch G**, Ferrero EM, Fisher RE (2012) The head and neck muscles of the serval and tiger: Homologies, evolution, and proposal of a mammalian and a veterinary muscle ontology. The Anatomical Record **295** (12): 2157-2178. IF = 1,343.

7. Diogo R, Potau JM, Pastor JF, de Paz F, Barbosa MM, Ferrero EV, **Bello G**, Aziz MA, Burrows A, Wood BA (2013). Photographic and descriptive atlas of orangutans (Pongo) - with notes on the attachments, variations, innervation, synonymy and weight of the muscles. Taylor & Francis (Oxford, UK).

8. Diogo R, Potau JM, Pastor JF, de Paz F, Barbosa MM, Ferrero EV, **Bello G**, Aziz MA, Burrows A & Wood BA (2013) Photographic and descriptive atlas of chimpanzees (Pan) - with notes on the attachments, variations, innervation, synonymy and weight of the muscles. Taylor & Francis (Oxford, UK).

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"What is a scientist after all? It is

a curious man looking through a

keyhole, the keyhole of nature,

trying to know what’s going on"

Jacques Cousteau

II. Discusión

1. INTERPRETACIÓN DE LOS RESULTADOS

1.1. Cautividad *vs*. libertad

La mayoría de colecciones osteológicas están constituidas por esqueletos de animales procedentes de medios de cautividad, especialmente en el caso de especies en peligro de extinción. Estas colecciones son esenciales para la mayoría de estudios morfológicos y funcionales. Sin embargo, existe una tendencia a rechazarlas al considerar que las condiciones de cautividad afectan de un modo significativo a la morfología de los huesos. Según este punto de vista los individuos procedentes de cautividad no se consideran representativos de las especies en su conjunto y, por tanto, las conclusiones morfológicas y funcionales obtenidas a partir de este tipo de colecciones no se consideran fiables (O'Regan 2001; O'Regan & Kitchemer 2005). Algunos estudios han intentado comprender la influencia de las condiciones de cautividad en la morfología del hueso, aunque la mayoría de ellos se centraron en el cráneo de diferentes especies de mamíferos (Hollister 1917; Groves 1982; O'Regan 2001; Zuccarelli 2004). No obstante, la influencia de la cautividad nunca había sido analizada en el caso de las escápulas de los primates.

El análisis de la morfometría geométrica en 2D realizado sobre la cara dorsal de la escápula de varias especies de primates hominoideos (Bello-Hellegouarch *et al*. 2013b) no detectó diferencias significativas entre los especímenes procedentes de cautividad y de libertad para ninguna de las especies analizadas (*Figura 25*).

Este resultado sugiere que la cautividad no afecta significativamente a la morfología de la escápula. Por lo tanto, las escápulas de especímenes en cautividad pueden ser empleadas en estudios morfológicos como representantes fiables de las escápulas de las especies en su totalidad, sin riesgo a estar analizando ejemplares no representativos de las especies de interés, al menos para las especies analizadas. Sin embargo, estos resultados no son extrapolables a otras regiones anatómicas, ya que los diferentes huesos pueden responder de un modo diferente a los mismos estímulos externos (Biewener & Gillis 1999; Pearson & Lieberman 2004; Plochocki *et al*. 2008; Green *et al*. 2012). Este es el caso, por ejemplo, de la ulna de *Pithecia pithecia*, cuya morfología se ve alterada por las frecuentes actividades cuadrúpedas a las que se ven forzados estos animales debido al pequeño tamaño de sus jaulas (Fleagle & Meldrum 1988). En este sentido, la morfometría geométrica parece ser una herramienta extremadamente útil para determinar el impacto de la cautividad sobre la morfología del hueso. De este modo resultaría de enorme interés el empleo de esta metodología en otros huesos del esqueleto postcraneal con el fin de identificar con precisión si las condiciones de cautividad afectan de manera diferente a las diversas regiones anatómicas.

Sin embargo, no podemos descartar la posibilidad de que las condiciones de una vida en cautividad afecten significativamente a los músculos del hombro mientras que la morfología de la escápula se mantiene intacta, ya que los músculos son más susceptibles que los huesos ante las diferentes condiciones del hábitat y las diferencias comportamentales (Ward & Sussman 1979). Sería de gran interés, por tanto, comparar la musculatura del hombro de primates procedentes tanto de cautividad como de libertad. Aunque ya se han realizado algunos estudios acerca de la musculatura del hombro en primates (Potau *et al*. 2009; Myatt *et al*. 2012) y en organismos modelo como ratones (Green *et al*. 2012), todos se han realizado con especímenes en cautividad. Resulta extremadamente complicado obtener datos similares de animales en libertad, debido a la dificultad de conseguir cadáveres y a los problemas éticos relacionados con el estudio de animales en peligro de extinción en su medio natural.

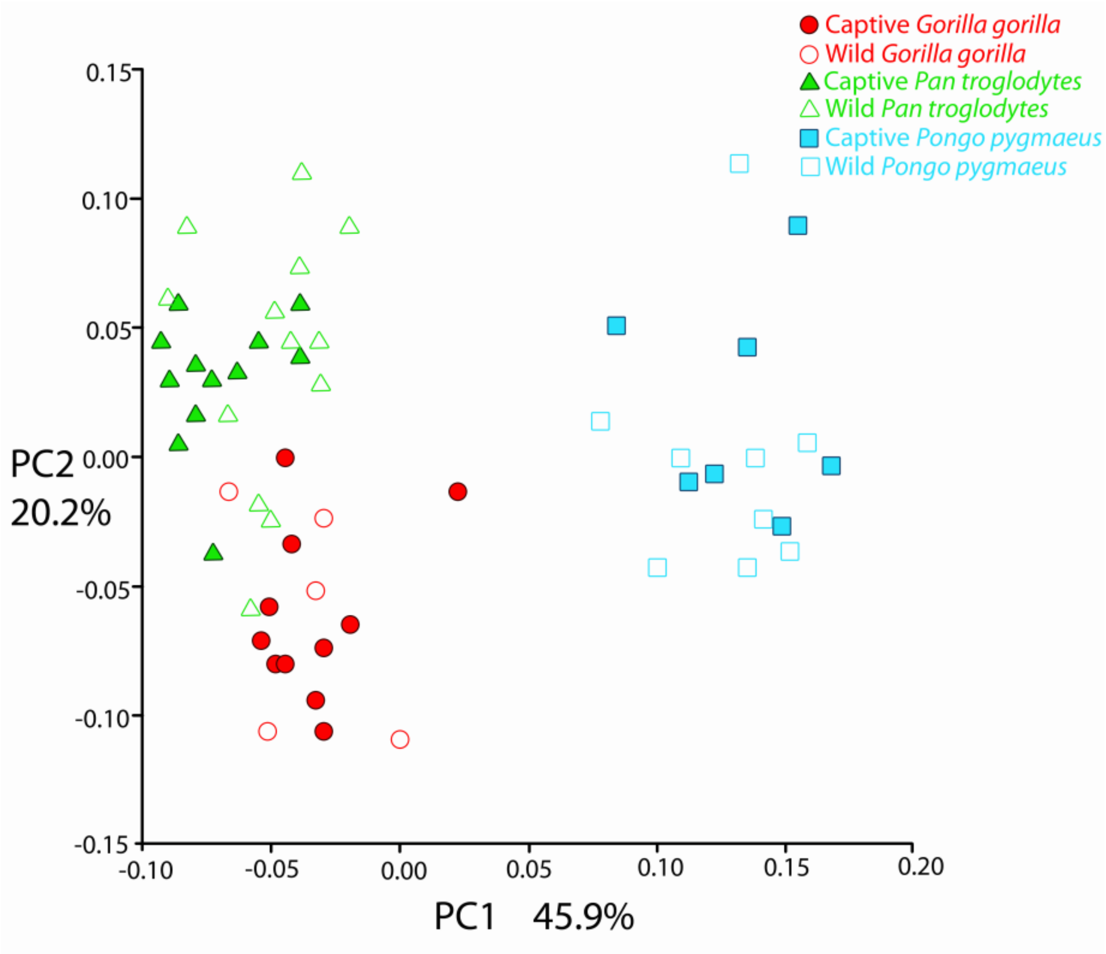

Figura 25. *Dispersión de las tres especies analizadas (*Gorilla gorilla*,* Pan troglodytes *y* Pongo pygmaeus*) para los dos primeros PCs (PC1 y PC2); se observa el gran solapamiento entre los individuos de libertad (símbolos huecos) y los individuos de cautividad (símbolos rellenos) (imagen procedente de Bello-Hellegouarch* et al*. 2013b, p 308).*

1.2. Morfología y función

Los primates pueden clasificarse, en función de su plan corporal, en ortógrados o pronógrados. Los primates ortógrados (gorilas, chimpancés, orangutanes, gibones y humanos) se caracterizan por adaptaciones anatómicas en el esqueleto postcraneal relacionadas con la vida arbórea y modos de desplazamiento suspensorios, como son la columna dispuesta verticalmente, tórax ancho y aplastado dorsoventralmente, escápula situada dorsalmente, cavidad glenoidea orientada ventrolateralmente y cranealmente para aumentar la movilidad de la articulación glenohumeral, etc. (Aiello & Dean 1990; Larson 1993; Gebo 2010). Los primates pronógrados, por el contrario, presentan el plan corporal típico de la mayoría de los mamíferos terrestres cuadrúpedos, caracterizado por un tórax cilíndrico y estrecho, con las extremidades situadas ventralmente y las escápulas situadas en el plano parasagital, y la articulación glenohumeral con escasa movilidad (Fleagle 1999; Gebo 2010). De este modo, aunque los músculos del manguito rotador ejercen funciones similares en todas las especies de primates (explicadas en los apartados 2 y 3 de la *Introducción*), algunas de estas funciones son más importantes que otras en relación con el tipo de locomoción principal.

Las características básicas de la función muscular se pueden conocer analizando la expresión de las diferentes isoformas de la cadena pesada de la miosina (MHC). Como vimos en el apartado 4.3 de la *Introducción*, existen isoformas asociadas con músculos resistentes a la fatiga (MHC-I) e isoformas asociadas con músculos de contracción rápida pero poco resistentes (MHC-IIa y MHC-IIx). Su análisis nos ha permitido demostrar que el músculo supraespinoso de los primates pronógrados no expresa la isoforma más rápida y menos resistente MHC-IIx (Potau *et al*. 2011), que normalmente no se expresa en músculos lentos y posturales (Fitts *et al*. 1991; Baldwin 1996; Fitts & Widrick 1996; Schiaffino & Reggiani 1996; Rivero *et al*. 1999; Talmadge 2000). Por tanto, este resultado proporciona evidencias moleculares de la importancia del músculo supraespinoso como músculo postural (estabilizador de la articulación glenohumeral) en los primates pronógrados (Potau *et al*. 2011), aunque en la sección 1.2.2 de la *Discusión* se discute con detalle la función de este músculo y las adaptaciones morfológicas de la escápula en los diferentes grupos locomotores de primates pronógrados. En cambio, hemos podido constatar que los primates ortógrados, incluidos los humanos, expresan las tres isoformas de MHC, con un mayor porcentaje de las dos isoformas rápidas MHC-II que de la isoforma lenta y resistente MHC-I (Potau *et al*. 2011, 2012). Este patrón de expresión es típico de músculos rápidos y potentes con una baja resistencia a la fatiga (Klitgaard *et al*. 1990; Harridge *et al*. 1996), por lo que este resultado proporciona evidencia molecular de la función elevadora, no postural, del músculo supraespinoso en los primates ortógrados (Potau *et al*. 2011).

Sin embargo, aunque los primates ortógrados emplean varios modos de locomoción (braquiación, *arm-swinging*, *knuckle-walking*, etc.) no se han observado diferencias en los patrones de expresión de las isoformas de MHC en relación con estos tipos de locomoción (Potau *et al*. 2011), diferencias que sí se han detectado en los pesos musculares y la morfología de la escápula (Bello-Hellegouarch *et al*. 2013a), y que se discuten en los apartados 1.2.1 y 1.3 de esta *Discusión*. Resulta interesante la existencia de diferencias significativas en los patrones de expresión de las isoformas de MHC entre los primates ortógrados *knuckle-walkers* y los pronógrados cuadrúpedos (tanto arbóreos como semiterrestres), a pesar de ser todos cuadrúpedos (Potau *et al*. 2011). Este resultado nos indica que la actividad electromiográfica del músculo supraespinoso de chimpancés y gorilas (Tuttle & Basmajian 1978a,b; Larson & Stern 1987) no está relacionada con un patrón de expresión de MHC de tipo pronógrado (Potau *et al*. 2011).

Los análisis de la expresión diferencial de las isoformas de MHC en los músculos de primates con diferentes tipos de locomoción resultan útiles para obtener información adicional sobre las adaptaciones locomotoras de la escápula y los músculos del manguito rotador. Por el momento hemos realizado estos análisis únicamente en el músculo supraespinoso (Potau *et al*. 2011, 2012), pero estamos realizando el mismo tipo de análisis en el resto de músculos del manguito rotador.

1.2.1. Primates ortógrados

El análisis de la morfometría geométrica (GM) de la escápula (Bello-Hellegouarch *et al*. 2013a) permitió detectar diferencias significativas entre grupos locomotores, siendo estos resultados consistentes con estudios previos (Young 2008), de modo que los gibones (*Hylobates*) difieren claramente del resto de primates hominoideos, los humanos (*Homo*) y los orangutanes (*Pongo*) comparten morfologías y se diferencian de los gorilas (*Gorilla*) y los chimpancés (*Pan*), que presentan escápulas próximas a las de los gorilas (*Figura 26*).

Las principales diferencias detectadas en la forma de la escápula se relacionan con la variación en la proporción entre las fosas supraespinosa e infraespinosa y con la inclinación y longitud relativa de la espina de la escápula (Bello-Hellegouarch *et al*. 2013a). Estos dos parámetros están directamente relacionados ya que, aunque otros músculos que se insertan en la espina de la escápula influyen en cierta medida en su orientación (p. ej. el deltoides y el trapecio), la orientación de la espina de la escápula en primates suspensorios está directamente relacionada con los músculos dorsales del manguito rotador (supraespinoso e infraespinoso) y con el papel que juegan durante la elevación de la extremidad anterior y la suspensión (Larson & Stern 1986; Larson *et al*. 1991; Bello-Hellegouarch *et al*. 2012).

Los *knuckle-walkers* (*Gorilla* y *Pan*) tienen una espina con un ángulo menos inclinado que los gibones pero más que los orangutanes y humanos (*Figura 26*), con una fosa supraespinosa relativamente grande, especialmente en *Gorilla* (Schultz 1930; Roberts 1974; Aiello & Dean 1990; Potau *et al*. 2007; Young 2008; Bello-Hellegouarch *et al*. 2012, 2013a). Esta gran fosa supraespinosa podría estar relacionada con el papel esencial que el músculo supraespinoso juega como músculo postural durante el *knuckle-walking*, actuando junto con el músculo infraespinoso en la estabilización de la articulación glenohumeral y controlando la retracción del húmero durante la fase de soporte (Roberts 1974; Tuttle & Basmajian 1978b; Larson & Stern 1987, 1992; Potau *et al*. 2009; Bello-Hellegouarch *et al*. 2012).

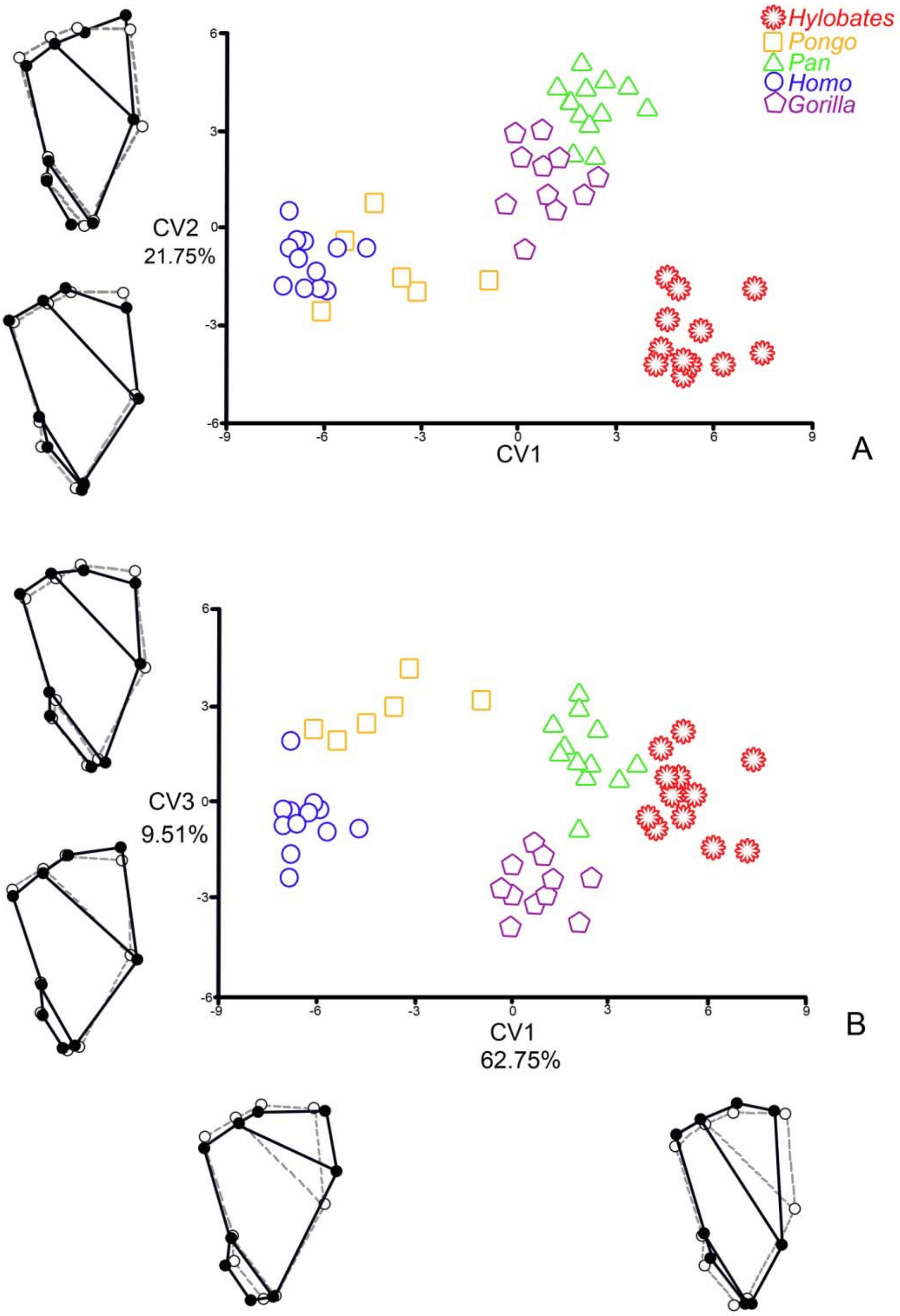

Figura 26. *Dispersión de los* canonical variates *(CV) para los grupos locomotores (a) CV1 vs. CV2 y (b) CV1 vs. CV3. Las formas escapulares con trazos negros muestran las formas de cada extremo del CV, mientras que las formas con trazos discontinuos grises representan la forma media (coordenadas 0, 0) (Imagen procedente de Bello-Hellegouarch* et al*. 2013a, p 324).*

El músculo supraespinoso también interviene resistiendo las tensiones de cizalla que actúan sobre la articulación glenohumeral provocadas por la posición dorsal de la escápula de los *knuckle-walkers* (Roberts 1974; Larson 1993).Las diferencias que encontramos entre gorilas y chimpancés, ambos *knuckle-walkers*, podrían explicarse por sus diferencias locomotoras. Los chimpancés son altamente arbóreos, aunque pasan mucho tiempo en el suelo como *knuckle-walkers* (Goodall 1965; Fleagle 1999; Ward 2007), mientras que los gorilas son trepadores ocasionales de hábitos más terrestres que los chimpancés (Tuttle & Watts 1985; Remis 1995; Fleagle 1999; Ward 2007), especialmente las hembras del gorila occidental de llanura (Tutin & Fernandez 1985; Kuroda 1992; Doran 1996).

La hipertrofia del músculo supraespinoso de los gorilas podría estar relacionada con una mayor frecuencia de hábitos cuadrúpedos terrestres de tipo *knuckle-walker*, que combinados con su gran tamaño, determinan una enorme necesidad de estabilización de la articulación glenohumeral (Bello-Hellegouarch *et al*. 2013a). Esta diferencia de tamaño relativo del músculo supraespinoso entre chimpancés y gorilas se confirmó con el análisis de los pesos musculares (Potau *et al*. 2011). El músculo supraespinoso de los gorilas está hipertrofiado en comparación con el de los chimpancés. Aunque se ha sugerido que gran parte de la variación interespecífica en la morfología y comportamiento de gorilas y chimpancés podría deberse a diferencias de tamaño (Doran 1997; Isler 2005), algunos rasgos anatómicos, especialmente los relacionados con las diferencias comportamentales y locomotoras, no se pueden explicar por esa diferencia (Doran 1997).

Los humanos son los hominoideos con la espina de la escápula con menor inclinación (*Figura 26*) y, por tanto, con la mayor diferencia de tamaño entre las fosas supraespinosa e infraespinosa (Bello-Hellegouarch *et al*. 2012, 2013a). En humanos modernos la posición colgante habitual de la extremidad anterior y su uso casi exclusivo como órgano manipulador (Larson 1993, 1995; Potau *et al*. 2011) han reducido las tensiones de cizalla que actúan sobre la articulación glenohumeral, reduciendo la necesidad de tener un músculo altamente desarrollado. De este modo, la fosa supraespinosa de los humanos está poco desarrollada (Roberts 1974; Potau *et al*. 2007; Bello-Hellegouarch *et al*. 2012, 2013a), igual que el músculo supraespinoso (Potau *et al*. 2011). Este escaso desarrollo del músculo supraespinoso permite el aumento de velocidad y precisión de los movimientos de la articulación glenohumeral, lo que es favorable para la función manipuladora de la extremidad anterior (Potau *et al*. 2007).

Sin embargo, al mismo tiempo que aumenta la velocidad y precisión de los movimientos de la articulación, se reduce la habilidad para elevar la extremidad anterior en comparación con el resto de primates hominoideos (Ashton & Oxnard 1963, 1964; Oxnard 1967, 1969; Larson 1993; Bello-Hellegouarch *et al*. 2012). Esta naturaleza rápida y poco resistente del músculo supraespinoso se confirma por estudios electromiográficos (Basmajian & de Luca 1985) y por la expresión más elevada de las isoformas rápidas de MHC-II (incluyendo la más rápida de todas, la MHC-IIx) en humanos (Potau *et al*. 2011, 2012). Por otro lado, el músculo infraespinoso de los humanos está relativamente bien desarrollado en comparación con el músculo supraespinoso (Roberts 1974; Aiello & Dean 1990).

Esto es debido a la necesidad de rotación externa durante la elevación de la extremidad anterior en el plano escapular, con el fin de retrasar el contacto entre el acromion y el tubérculo mayor del húmero (Inman *et al*. 1944; Basmajian & de Luca 1985).

Los orangutanes, altamente arbóreos y suspensores, se muestran más cercanos a los humanos en el análisis de GM que a los *knuckle-walkers* y a los gibones (Bello-Hellegouarch *et al*. 2013a). Su escápula se caracteriza por una espina escasamente angulada y una fosa supraespinosa pobremente desarrollada en comparación con la fosa infraespinosa (*Figura 26*) (Roberts 1974; Oxnard 1984; Young 2008; Bello-Hellegouarch *et al*. 2012, 2013a). La relativamente bien desarrollada fosa del músculo infraespinoso confirma el papel esencial de este músculo en los comportamientos suspensores. Por un lado, actúa como rotador externo (lateral) de la extremidad anterior (asistido por el músculo redondo menor) durante la *swing phase* del *vertical climbing*, mientras que, por otro, actúa como estabilizador de la articulación glenohumeral durante la *pendant suspension* y durante la fase de soporte del *arm-swinging* (Larson & Stern 1986).

En los hilobátidos la espina de la escápula muestra una inclinación máxima (*Figura 26*), de modo que las fosas supraespinosa e infraespinosa tienen tamaños similares. Esta hipertrofia de la fosa supraespinosa no puede deberse a una función postural, como en los *knuckle-walkers*, ya que nunca emplean la cuadrupedia como modo de locomoción, sino a las enormes especializaciones del hombro de los hilobátidos relacionadas con la braquiación (Young 2008). Para alcanzar un soporte elevado durante el *vertical climbing*, los gibones muestran un grado de abducción del húmero mayor que en los grandes simios, probablemente debido a la escasa torsión de la cabeza del húmero en los gibones (Isler 2002, 2005). Por tanto, la gran fosa supraespinosa podría deberse a la necesidad de un gran músculo abductor con ese fin (Bello-Hellegouarch *et al*. 2013a). Algunos estudios han sugerido que los abductores del hombro de los braquiadores (hilobátidos) son especialmente importantes para realizar rápidas aceleraciones de la extremidad anterior, y para alcanzar soportes situados por encima de la cabeza que no se encuentran exactamente en el plano sagital del cuerpo (Michelsens *et al*. 2009, 2010). Además, el músculo infraespinoso, al igual que los rotadores de la escápula, tiene una función fundamental en la estabilización del cuerpo durante la braquiación, evitando que se balancee mediolateralmente en lugar de anterioposteriormente (Michelsen *et al*. 2009; Kikuchi *et al*. 2012). Las diferencias encontradas en la forma de las escápulas entre orangutanes y gibones pueden deberse a diferencias en sus comportamientos locomotores, a pesar de que ambos taxones tengan hábitos arbóreos estrictos. Los orangutanes, debido a su gran tamaño y peso, adoptan un modo más lento y cauteloso de locomoción suspensoria cuadrumana, empleando las extremidades anteriores y posteriores (Fleagle 1999; Thorpe y Crompton 2005, 2006; Ward 2007). Los gibones, pequeños y ligeros, impulsan su cuerpo de un modo rápido y efectivo a través del dosel mediante braquiación, sin el uso de las extremidades posteriores (Napier 1963; Tuttle 1975; Fleagle 1999).

Las diferencias encontradas en las proporciones entre las fosas supraespinosa e infraespinosa de los grupos locomotores de los primates ortógrados permiten especular acerca de la evolución del comportamiento locomotor en hominoideos (Bello-Hellegouarch *et* *al*. 2013a). El enorme parecido entre los orangutanes (*Pongo*) y los humanos (*Homo*) sugiere que el último ancestro común del clado chimpancé-humano probablemente mostraba un patrón general del hombro propio de animales suspensores (Oxnard 1984; McHenry 1986; Thorpe *et al*. 2007; Crompton *et al*. 2008, 2010; Kivell & Schmitt 2009), en lugar de una estructura propia de *knuckle-walker*, como se ha sugerido frecuentemente (Begun 1992; Richmond & Strait 2000; Corruccini & McHenry 2001; Richmond *et al*. 2001; Orr 2005; Williams 2010). Además, a pesar de las similitudes encontradas entre los gorilas (*Gorilla*) y los chimpancés (*Pan*), presentan patrones morfológicos diferenciados, apoyando la evolución independiente del *knuckle-walking* en los dos taxones (Larson 1996; Dainton & Macho 1999; Kivell & Schmitt 2009), sugiriendo una homoplasia entre *Pan* y *Gorilla*. Finalmente, el hecho de que los gibones (*Hylobates*) se encuentren completamente separados de los otros grupos apoya la hipótesis altamente aceptada de que los hilobátidos fueron los primeros hominoideos en divergir (Groves 1972; Tuttle 1975; Ruvolo 1997; Young 2003). Prueba de esto son las múltiples autapomorfías, como un reducido tamaño corporal combinado con especializaciones para la braquiación altamente derivadas (Cartmill 1985), que los diferencian del resto de hominoideos más generalizados.

1.2.2. Primates pronógrados

Entre los factores externos que pueden potencialmente influir en la forma de la escápula de los primates pronógrados (Bello-Hellegouarch *et al*. *en revisión*), la locomoción es el que muestra mayor correlación con ella, seguido de la filogenia a nivel de familia (*Figura 27*). Aunque existe una clara agrupación relacionada con la historia evolutiva de las especies (generalmente las especies de una misma familia tienen escápulas similares) el modo de locomoción tiene una elevada influencia sobre la morfología de la escápula. Así, *Lagothrix*, en lugar de situarse cerca de los otros atélidos (*Ateles* y *Alouatta*), permanece próximo a especies con modos de locomoción cuadrúpedos arbóreos más estrictos (p. ej. *Colobus guereza*, *Cercopithecus mitis* o *Cercopithecus ascanius*). Además, los prosimios (Lemuridae, Lorisidae, Tarsiidae, Galagidae), en lugar de compartir una forma escapular similar y permanecer juntos en el gráfico, muestran una elevada dispersión consistente con sus diversos modos de locomoción. Finalmente, los cercopitécidos muestran un gradiente en su distribución relacionado con el tipo de cuadrupedia: terrestre o arbórea.

Estos resultados concuerdan con otros estudios que indican que la señal filogenética en la escápula es más débil que la funcional (Young 2008; Preuschoft *et al*. 2010). Por consiguiente, la variación morfológica del esqueleto postcraneal (Pilbeam 1996; Ward 1997; Lockwood 1999; Collard *et al*. 2001) y del hombro en primates (Ashton & Oxnard 1963; Young 2008; Preuschoft *et al*. 2010) parece ser principalmente adaptativa, relacionada con la función durante la locomoción, más que determinada por la historia evolutiva del grupo. Estudios recientes sugieren que algunos aspectos morfológicos de la escápula se ven altamente influenciados por los estreses mecánicos, mostrando una naturaleza altamente adaptativa a las diferentes fuerzas resultantes de los diferentes modos de locomoción (Preuschoft *et al*. 2010; Green *et al*. 2012).

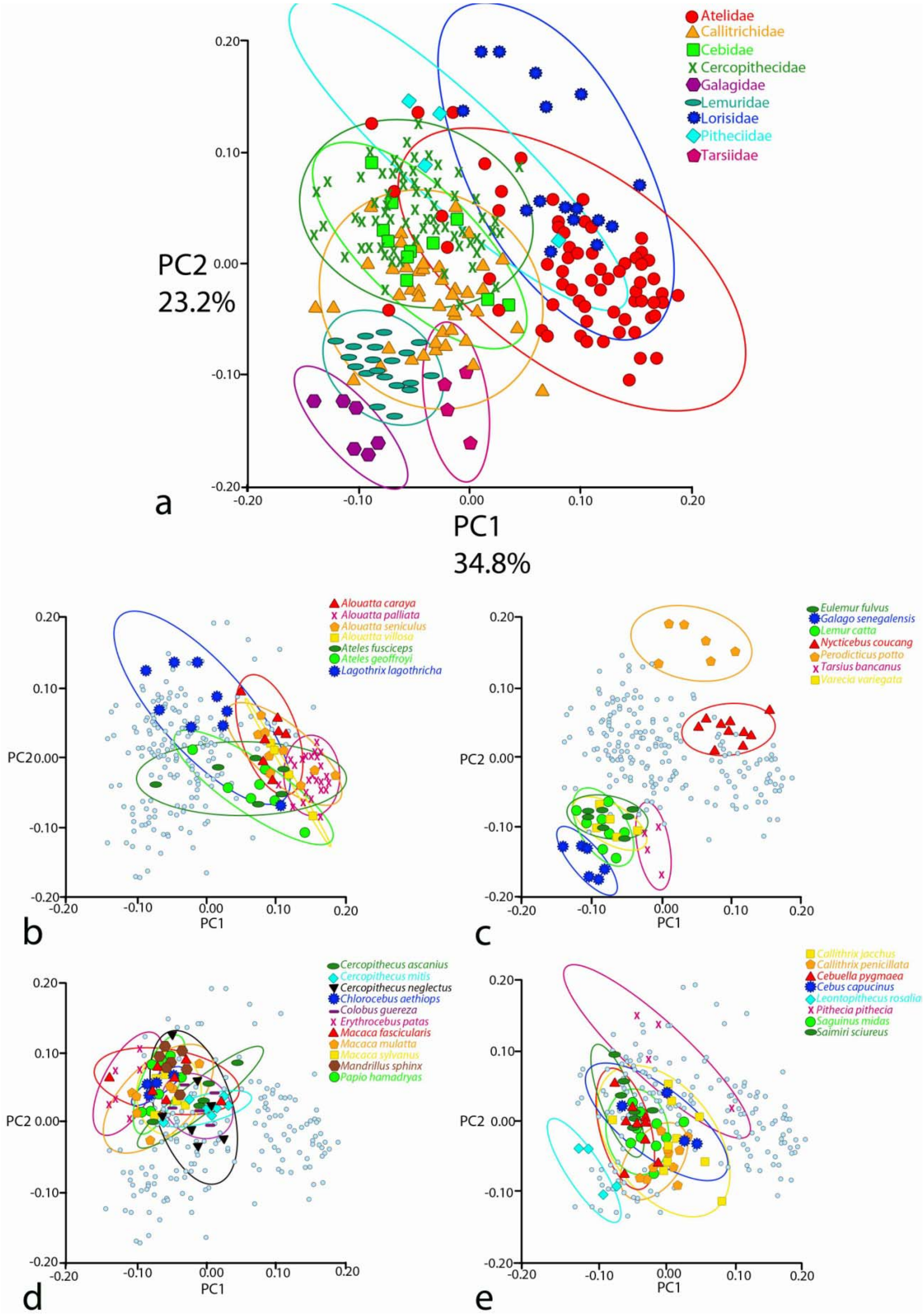
Atelidae
Callitrichidae
Cebidae
Cercopithecidae
Galagidae
Lemuridae
Lorisidae
Pitheciidae
Tarsiidae
PC2
23.2%
PC1
34.8%
a
Alouatta caraya
Alouatta palliata
Alouatta seniculus
Alouatta villosa
Ateles fusciceps
Ateles geoffroyi
Lagothrix lagothricha
b
Eulemur fulvus
Galago senegalensis
Lemur catta
Nycticebus coucang
Perodicticus potto
Tarsius bancanus
Varecia variegata
c
Cercopithecus ascanius
Cercopithecus mitis
Cercopithecus neglectus
Chlorocebus aethiops
Colobus guereza
Erythrocebus patas
Macaca fascicularis
Macaca mulatta
Macaca sylvanus
Mandrillus sphinx
Papio hamadryas
d
Callithrix jacchus
Callithrix penicillata
Cebuella pygmaea
Cebus capucinus
Leontopithecus rosalia
Pithecia pithecia
Saguinus midas
Saimiri sciureus
e
PC1
PC2
0.20
0.10
0.00
-0.10
-0.20

Figura 27. *Dispersión de los dos primeros componentes principales (PC1 y PC2) derivados del análisis de morfometría geométrica de las escápulas de los primates pronogrados realizado en Bello-Hellegouarch* et al*.* en revisión*. A: distribución de las nueve familias de primates pronógrados incluidas en el estudio (Atelidae, Callitrichidae, Cebidae, Cercopithecidae, Galagidae, Lemuridae, Lorisidae, Pitheciidae y Tarsiidae); B: detalle de la distribución de las siete especies de Atelidae analizadas (*Alouatta caraya, Al. palliata, Al. seniculus, Al. villosa, Ateles fusciceps, At. geoffroyi *y* Lagothrix lagothricha*); C: detalle de la distribución de las siete especies de prosimios (Galagidae, Lemuridae, Lorisidae y Tarsiidae) analizadas (*Eulemur fulvus, Galago senegalensis, Lemur catta, Nycticebus coucang, Perodicticus potto, Tarsius bancanus *y* Varecia variegata*); D: detalle de la distribución de las once especies de Cercopithecidae analizadas (*Cercopithecus ascanius, C. mitis, C. neglectus, Chlorocebus aethiops, Colobus guereza, Erythrocebus patas, Macaca fascicularis, M. mulatta, M. sylvanus, Mandrillus sphinx *y* Papio hamadryas*); E: detalle de la distribución de las cinco especies de Callitrichidae (*Callithrix jacchus, Ca. penicillata, Cebuella pygmaea, Leontopithecus rosalia *y* Saguinus midas*), la especie de Pitheciidae (*Pithecia pithecia*) y las dos especies de Cebidae (*Cebus capucinus *y* Saimiri sciureus*)analizadas.*

Los primates *cuadrúpedos terrestres* realizan posturas locomotoras con los brazos extendidos, en aducción, con la articulación del hombro limitada para realizar movimientos anteroposteriores en el plano parasagital (Roberts 1974; Fleagle 1999). El peso del cuerpo actúa comprimiendo la articulación glenohumeral durante la fase de soporte, asegurando su integridad (Roberts & Davidson 1975; Jouffroy *et al*. 1990; Whitehead & Larson 1994). En cambio, los primates *cuadrúpedos arbóreos* se mueven a través de un medio tridimensional y discontinuo, de modo que requieren una articulación del hombro más móvil para usar las extremidades anteriores en posturas de abducción (Roberts & Davidson 1975; Fleagle 1999). Por lo tanto, los músculos del manguito rotador y sus fosas, especialmente el músculo supraespinoso, estarán más desarrollados en los primates cuadrúpedos arbóreos que en los terrestres (Roberts 1974; Roberts & Davidson 1975; Manaster 1979; Larson & Stern 1987, 1989, 1992). Sin embargo nuestros resultados no son consistentes con esta explicación, ya que observamos que los cuadrúpedos terrestres comparten una fosa supraespinosa relativamente más grande y una espina escapular más larga que la de los cuadrúpedos arbóreos (Figura 28a, c). Esto podría estar relacionado con la necesidad de estabilización de la articulación glenohumeral para resistir las fuerzas de compresión que se generan entre el sustrato y las extremidades anteriores durante la fase de soporte de la locomoción cuadrúpeda terrestre (Oxnard 1967, 1976; Kimes *et al*. 1981; Larson & Stern 1989, 1992; Whitehead & Larson 1994; Preuschoft *et al*. 2010; Potau *et al*. 2011). La escápula relacionada con la *cuadrupedia semiterrestre* (Figura 28b) presenta una forma intermedia entre las escápulas de los cuadrúpedos arbóreos y los terrestres, lo que concuerda con estudios previos (Anapol & Gray 2003). El músculo redondo mayor ayuda a retraer el húmero con el fin de elevar la mano lejos del sustrato durante la transición entre la fase de soporte y la *swing phase* (Larson & Stern 1989, 2007; Whitehead & Larson 1994). Sin embargo, las diferencias son muy sutiles, siendo la forma de la escápula de todos los cuadrúpedos muy similar. Las diferencias entre cuadrúpedos terrestres, semiterrestres y arbóreos parecen ser significativamente mayores en los músculos de la extremidad anterior que en los del hombro (Anapol & Gray 2003).

Durante la *suspensión bimanual* realizada por *Ateles* (mono araña) y, en menor medida, por *Lagothrix* (mono lanudo), las extremidades anteriores están completamente extendidas por encima de la cabeza. Para reforzar su capacidad de movimiento en todas las direcciones, su escápula, relativamente corta y ancha (Figura 28d), está situada dorsalmente en la caja torácica en lugar de lateralmente, lo que los diferencia totalmente del resto de primates pronógrados, que tienen la escápula situada en el plano parasagital (Larson 1993; Fleagle 1999). Los atélidos suspensores, especialmente *Ateles*, han sufrido una convergencia con los hominoideos en su anatomía postcraneal debido a este comportamiento suspensor (Erikson 1963; Andrews & Grove 1976; Corrucini & Ciochon 1978; Larson 1998). Sin embargo, los platirrinos suspensores se diferencian de los hominoideos principalmente en la utilización de su cola prensil que actúa como un quinto brazo durante la fase de soporte de la progresión bimanual (Carpenter & Durham 1969; Mittermeier & Fleagle 1976; Mittermeier 1978). Su articulación glenohumeral debe ser altamente móvil para realizar libremente multitud de movimientos con el fin de alcanzar las ramas situadas por encima de la cabeza. Por ello, estos animales requieren un músculo infraespinoso bien desarrollado, el principal estabilizador de la articulación glenohumeral durante la *pendant suspension* y la fase de soporte del *arm-swinging* (Roberts 1974; Larson & Stern 1986; Larson 1995). La fosa supraespinosa es amplia, pero no tanto como se esperaba en un primate suspensor que realiza actividades anti-pronógradas, con las extremidades anteriores en posturas elevadas y abducidas (Cant 1986; Larson & Stern 1986, 1987). La abducción del brazo en los platirrinos suspensores es realizada principalmente por el músculo deltoides, lo que hace innecesario un músculo supraespinoso extremadamente hipertrofiado (Youlatos 2000).

La *suspensión cuadrúpeda* (Figura 28e), típica de primates arbóreos como los lorísidos y *Ateles*, se caracteriza por un desplazamiento horizontal por debajo del sustrato en una posición invertida, empleando las cuatro extremidades en tensión (Napier 1967; Hunt *et al*. 1996; Fujiwara *et al*. 2011). Los requerimientos de los músculos del hombro en este tipo de locomoción son similares a los encontrados en la *suspensión bimanual*, es decir, un músculo infraespinoso relativamente grande para estabilizar la articulación glenohumeral (Roberts 1974; Larson & Stern 1986; Larson 1995) y un músculo supraespinoso relativamente bien desarrollado para abducir y elevar la extremidad anterior (Larson & Stern 1986, 1987). Sus ligeramente menores fosas en comparación las de las escápulas de los primates que realizan *suspensión bimanual*, se pueden explicar debido a la participación de las extremidades posteriores en la progresión del desplazamiento, a diferencia del caso de la *suspensión bimanual*, en la que sólo las extremidades anteriores participan en la locomoción.

El *pronograde clambering* se diferencia de la cuadrupedia en la ausencia de un patrón de marcha constante (*gait pattern*) y en que requiere una abducción de los brazos más pronunciada (Lockwood 1999; Youlatos 2000). Los caracteres morfológicos de su escápula (Figura 28f) son similares a las adaptaciones de la *suspensión bimanual*, con la fosa infraespinosa y del redondo mayor ligeramente más cortas, y la fosa supraespinosa significativamente grande por la enorme necesidad de abducción y elevación de la extremidad anterior durante este tipo de desplazamiento (Youlatos 2000).

El *slow-climbing quadrupedalism* consiste en una forma de locomoción cuadrúpeda lenta, suave y deliberada (Demes *et al*. 1990; Jouffroy & Petter 1990; Ishida *et al*. 1992). Durante la fase de soporte, mucho más larga que la *swing phase*, la articulación glenohumeral está tan abducida y rotada lateralmente que el tronco casi toca la rama (Ishida *et al*. 1992), requiriendo un músculo infraespinoso bien desarrollado y, por tanto, una gran fosa infraespinosa (Roberts 1974; Roberts & Davidson 1975; Gebo 1989). El músculo infraespinoso actúa como el principal sinergista del deltoides en movimientos que combinan rotación lateral con abducción del brazo (Larson & Stern 1986). Además, las especies que realizan este tipo de locomoción, como los lorísidos (*Nycticebus coucang* y *Perodicticus potto* en este estudio) se mueven a través de un soporte tridimensional, requiriendo una articulación glenohumeral móvil para alcanzar las ramas que se encuentran a diferentes alturas.Durante estos movimientos la estabilización de la articulación glenohumeral la realizan unos músculos supraespinoso e infraespinoso bien desarrollados (Figura 28g) (Oxnard 1967; Roberts & Davidson 1975; Larson & Stern 1986, 1989, 1992; Gebo 1989; Higurashi *et al*. 2007).

Menos evidentes son las adaptaciones al modo de locomoción conocido como *leaping* (Figura 28h), debido a que la mayoría de las adaptaciones extremas a este modo de locomoción se encuentran en las extremidades posteriores (Demes *et al*. 1996; Runestad Connour *et al*. 2000). El salto (*leap*) es llevado a cabo, fundamentalmente, por las extremidades posteriores y muchos *leapers* tienden a aterrizar con ellas también, mientras que las especies de mayor tamaño suelen aterrizar con las manos en primer lugar (Demes *et al*. 1996). Las extremidades anteriores de los *leapers* de gran tamaño, como *Lemur* o *Eulemur*, son particularmente importantes para el posicionamiento del cuerpo durante la aceleración que tiene lugar en el despegue (*takeoff*) y también durante la fase aérea del *leap*, durante la que levantan los brazos por encima de la cabeza con el fin de incrementar el momento de inercia de la parte anterior del cuerpo (Dunbar 1988; Demes *et al*. 1996; Terranova 1996). Por ello, la articulación glenohumeral de los *leapers* requiere cierta movilidad, que se consigue con una fosa supraespinosa relativamente bien desarrollada y una fosa infraespinosa mayor que en los pequeños y especializados *vertical clingers and leapers*, caracterizados por emplear la cola para ajustar la posición corporal en lugar de los brazos (Demes *et al*. 1996).

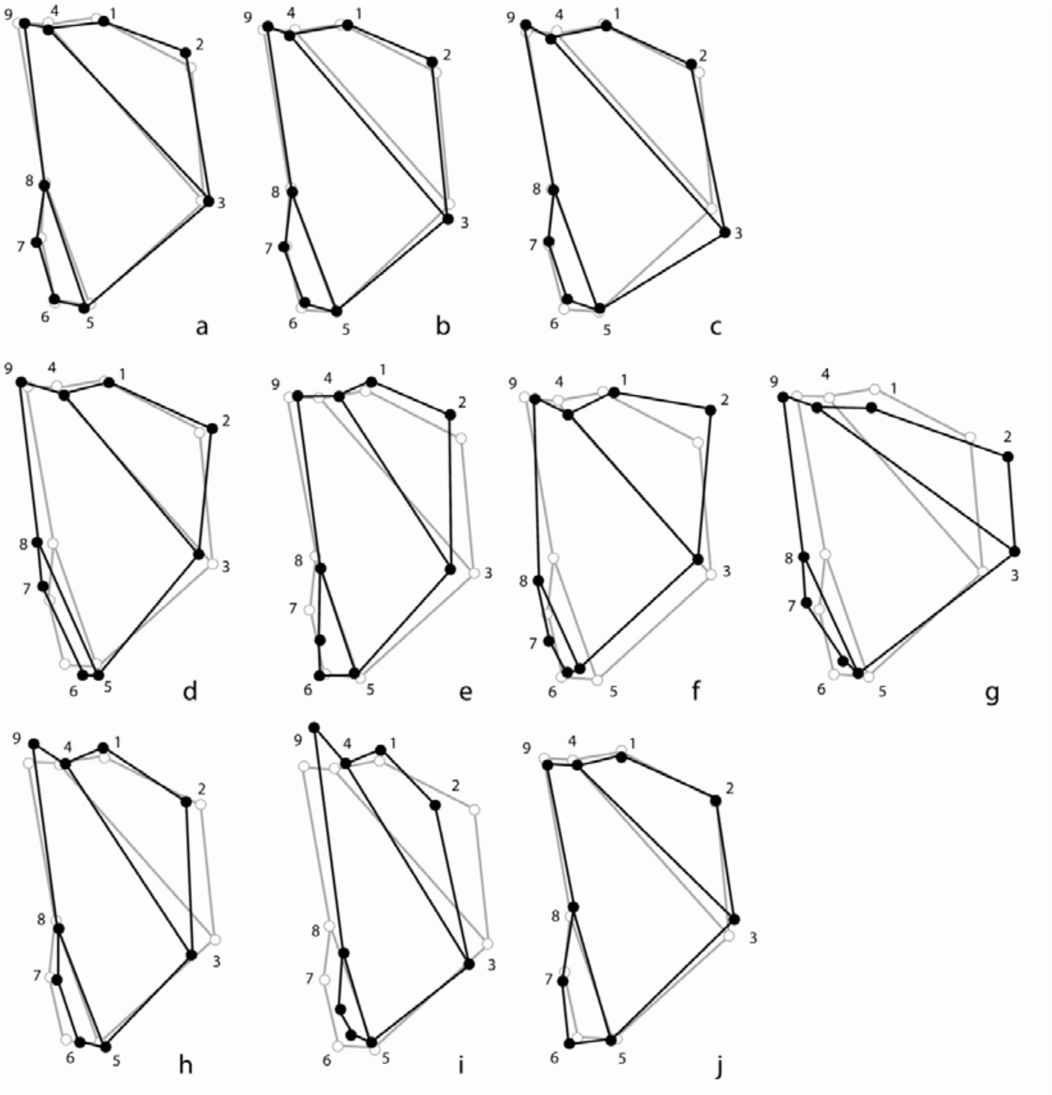

Figura 28. *Formas escapulares asociadas con cada modo de locomoción, extraídas del análisis de componentes principales realizado en Bello-Hellegouarch* et al. en revisión*. a: cuadrupedia arbórea; b: cuadrupedia semiterrestre; c: cuadrupedia terrestre; d: suspensión bimanual; e: suspensión cuadrúpeda; f:* pronograde clambering*; g:* slow-quadruped climbing*; h:* leaping*; i:* vertical clinging and leaping*; j:* vertical clinging*. La forma escapular asociada con cada modo de locomoción está representada mediante trazos negros, mientras que la forma media relacionada con el modo* climbing *se representa mediante trazos grises.*

En el *vertical clinging and leaping* las extremidades anteriores no se emplean directamente en el desplazamiento, por lo que estos animales no necesitan músculos del manguito rotador muy desarrollados, lo que les permite controlar los rápidos movimientos con precisión (Roberts & Davidson 1975; Higurashi *et al*. 2007). Sus escápulas son largas y estrechas, con fosas supraespinosa, infraespinosa y del redondo menor reducidas (Figura 28i). Aunque su articulación glenohumeral es capaz de realizar movimientos de elevación de la extremidad anterior, la capacidad de aducción y abducción es reducida (Roberts 1974; Roberts & Davidson 1975; Gebo 1989). La mayoría de adaptaciones de este tipo de locomoción se encuentran en las extremidades posteriores, más que en las anteriores (Demes *et al*. 1996; Runestad Connour *et al*. 2000).

El *vertical clinging* se caracteriza por una menor necesidad de estabilización del hombro por los músculos del manguito rotador (Fleagle & Meldrum 1988), con un músculo redondo mayor relativamente bien desarrollado. Este músculo es principalmente un aductor del húmero en relación con la escápula, muy importante durante el *climbing* y *clinging* (Fleagle & Meldrum 1988). Sin embargo, hemos observado una gran diferencia entre la escápula de los *vertical clingers* (Callitrichidae y *Pithecia*) y los *vertical clingers and leapers* (*Tarsius* y *Galago*), relacionada con la longitud de las fosas y de la espina de la escápula. Parece que los *vertical clingers* necesitan músculos supraespinoso, infraespinoso y redondo mayor relativamente más desarrollados (Figura 28j) que los *vertical clingers and leapers*, tal vez debido al empleo del *clinging* como modo de desplazamiento, mientras que los *vertical clinger and leapers* usan el *clinging* como comportamiento postural y saltan (*leap*) desde esa postura (Napier 1967; Napier & Walker 1967).

Las formas escapulares descritas son formas teóricas que reflejan las adaptaciones morfológicas relacionadas con tipos específicos de locomoción considerados independientemente para su mejor comprensión. Sin embargo, la mayoría de primates realizan más de un tipo de locomoción para desplazarse a través de su hábitat (Hunt *et al*. 1996; Fleagle 1999). Por tanto, la forma real de su escápula será el resultado de un compromiso entre los diferentes requerimientos de los diversos modos de locomoción que realizan. Por ejemplo, la escápula de los cuadrúpedos terrestres está caracterizada por una fosa supraespinosa relativamente más grande que la de los cuadrúpedos arbóreos (Bello-Hellegouarch *et al*. *en revisión*). Sin embargo, mucho estudios indican que en realidad los cuadrúpedos terrestres tienen una fosa supraespinosa relativamente más pequeña que los cuadrúpedos arbóreos, debido a que en los terrestres la proyección del tubérculo mayor del húmero aumenta el brazo de palanca del músculo supraespinoso, no necesitando un músculo de gran tamaño (Roberts 1974; Roberts & Davidson 1975; Manaster 1979; Larson & Stern 1987, 1989, 1992). Las especies que realizan cuadrupedia arbórea nunca realizan exclusivamente este modo de locomoción, sino que frecuentemente saltan, trepan o realizan otros modos de locomoción que requiere una fosa supraespinosa mayor que la que se espera en un cuadrúpedo arbóreo estricto. Además, hay que tener en cuenta que no existe una relación simple entre anatomía y comportamiento. Comportamientos similares pueden estar asociados a caracteres morfológicos diferentes, y caracteres anatómicos parecidos pueden cumplir los requisitos mecánicos de más de un comportamiento locomotor (Bock & von Wahlert 1965; Ward & Sussman 1979; Ruff & Runestad 1992; Fleagle 1999).

1.3. Métodos de medición del índice S/I

1.3.1. Fiabilidad de la discriminación de grupos locomotores

El índice S/I, es decir, la relación entre los tamaños de las fosas supraespinosa e infraespinosa, es una medida que se ha empleado frecuentemente en estudios relacionados con la morfología de la escápula y la función de los músculos del manguito rotador (Frey 1923; Schultz 1930; Inman *et al*. 1944; Roberts *et al*. 1974; Young 2008; Green *et al*. 2010; Bello-Hellegouarch *et al*. 2013a). Esto es debido a la estrecha relación que existe entre esta proporción y las diferencias funcionales de los diversos modos de locomoción de los primates. El modo clásico de calcular este índice consiste en medir la proporción entre las anchuras de ambas fosas, conocida como SFI (*spinal fossae index*, Frey 1923). Otro modo de obtener este índice puede ser considerando las áreas en 2D (2DI, a partir de fotografías) o en 3D (3DI, a partir de escaneados tridimensionales) de ambas fosas. Este enfoque se podría considerar, *a priori*, más fiable que clásico SFI, especialmente para el 3DI, que utiliza medidas reales de las áreas de las fosas y no sólo aproximaciones. El índice 3DI no ha sido utilizado en estudios previos a esta Tesis Doctoral.

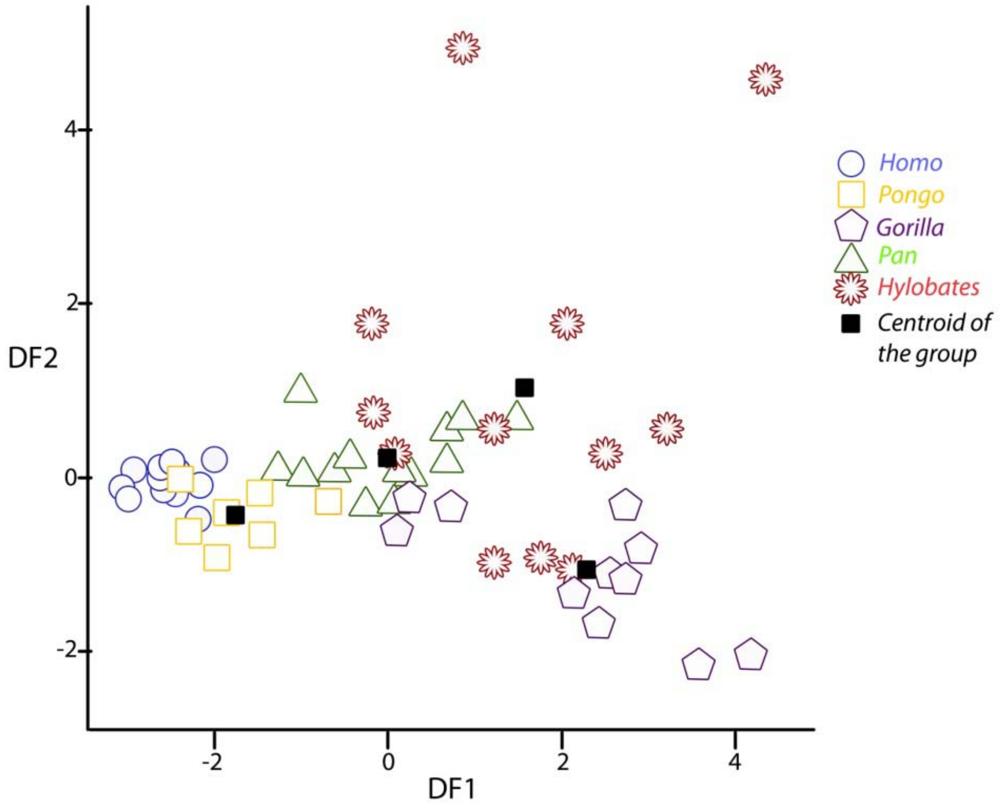

Figura 29. *Análisis Discriminante Lineal (LDA) de los tres índices estudiados (SFI, 2DI y 3DI) en Bello-Hellegouarch* et al*. 2013a (p 329).*

A la hora de discriminar por grupos locomotores los dos índices más eficaces son, efectivamente, el 2DI y el 3DI (*Figura 29*; Bello-Hellegouarch *et al*. 2013a). Los orangutanes (*Pongo*) y los humanos (*Homo*) presentan los valores más bajos para los tres índices analizados (SFI, 2DI, 3DI), un resultado que demuestra que estos dos grupos comparten la fosa supraespinosa más pequeña en relación con la fosa infraespinosa, comparados con los gorilas (*Gorilla*), los chimpancés (*Pan*) y los gibones (*Hylobates*). No existen diferencias significativas entre *Homo* y *Pongo* para ninguno de los tres índices, lo que concuerda con los resultados del análisis de morfometría geométrica (Bello-Hellegouarch *et al*. 2013a) en el que *Homo* y *Pongo* se solapan ligeramente. Sin embargo, los resultados obtenidos para *Pan*, *Hylobates* y *Gorilla* no son tan claros de interpretar. Hay diferencias significativas entre *Gorilla* y *Pan* para el 2DI, pero no entre *Gorilla* e *Hylobates*. No hay diferencias significativas para el 3DI entre *Gorilla* y *Pan* y tampoco entre *Gorilla* e *Hylobates*. Curiosamente, el análisis de morfometría geométrica encuentra similitudes entre *Gorilla* y *Pan* (Bello-Hellegouarch *et al*. 2013a), mientras que los índices 2DI y 3DI encuentran similitudes entre *Gorilla* e *Hylobates*. Además, aunque los índices 2DI y 3DI identifican *Gorilla* e *Hylobates* como los dos grupos con la fosa supraespinosa relativamente más grande de todos, el análisis de morfometría geométrica indentifica *Hylobates* con una fosa supraespinosa ligeramente mayor que la de *Gorilla*.

1.3.2. Hueso vs. *músculo*

La reconstrucción de comportamientos posturales y locomotores de especies extintas, especialmente las relacionadas con el origen de la especie humana, asumen que existe una relación directa entre el tamaño muscular y las inserciones musculares (Roberts 1974; Aiello & Dean 1990; Richmond & Strait 2000). Sin embargo, una parte sustancial de la información de los tejidos blandos se pierde al considerar solamente datos osteológicos, ya que el tamaño del músculo no refleja necesariamente el tamaño de la fosa o el área de inserción muscular. Hay multitud de factores, aparte del tamaño muscular, que pueden determinar el tamaño de la fosa y cuya influencia es prácticamente desconocida (Zumwalt 2006; Green 2010; Green *et al*. 2011), lo que complica la interpretación de la morfología de las inserciones musculares. Sin embargo, en las especies fósiles los huesos son la única evidencia disponible para analizar el patrón locomotor, por lo que resulta de gran importancia encontrar medidas osteológicas que sean buenas estimaciones de las medidas musculares. Con este fin, se compararon los índices entre la fosa supraespinosa y la infraespinosa (índice S/I) obtenidos de tres modos diferentes (SFI, 2DI, 3DI) con el índice S/I obtenido a partir de pesos musculares (*muscle weight index*, MWI), con el fin de determinar cuál de ellos se aproxima más al índice muscular.

De los tres índices S/I analizados a partir de datos osteológicos (SFI, 2DI y 3DI) el que más se aproxima a los valores musculares del índice MWI es el 3DI (Bello-Hellegouarch *et al*. 2013a), como se podría esperar, ya que las áreas tridimensionales de las fosas musculares se corresponden con los valores reales del tamaño de estas fosas, no con una aproximación o estimación de las mismas, como es el caso de los otros índices, el 2DI y el SFI.

Los humanos (*Homo*) siempre mostraron tanto la fosa como el músculo supraespinoso relativamente más pequeños en comparación con el resto de hominoideos. Los gibones (*Hylobates*) siempre presentaron la fosa supraespinosa relativamente más grande aunque los gorilas (*Gorilla*) presentaron el músculo supraespinoso más grande. También se observaron resultados contradictorios para los chimpancés (*Pan*) y los orangutanes (*Pongo*). En los especímenes disecados los tres índices coincidieron en que *Pongo* tiene una fosa supraespinosa relativamente más pequeña en comparación con *Pan*, pero el MWI demuestra que *Pongo* tiene un músculo supraespinoso relativamente más grande que *Pan*.

Estas discrepancias entre los datos osteológicos y musculares sugieren que hay que actuar con cautela al hacer inferencias sobre el tamaño muscular y los comportamientos locomotores basadas exclusivamente en análisis osteológicos. Se necesitan más estudios para comprender mejor la influencia del tamaño muscular sobre las inserciones en los huesos, especialmente si el objetivo es reconstruir modelos comportamentales a partir de datos osteológicos (Bello-Hellegouarch *et al*. 2013a). El índice 3DI demostró ser el índice más fiable para inferir patrones funcionales cuando los músculos están ausentes aunque los resultados obtenidos no siempre coinciden con los valores musculares.

2. PERSPECTIVAS FUTURAS

Esta Tesis Doctoral sirve como punto de partida de una investigación que puede aportar información valiosa sobre las adaptaciones funcionales de la escápula y los músculos del manguito rotador en el orden de los Primates.

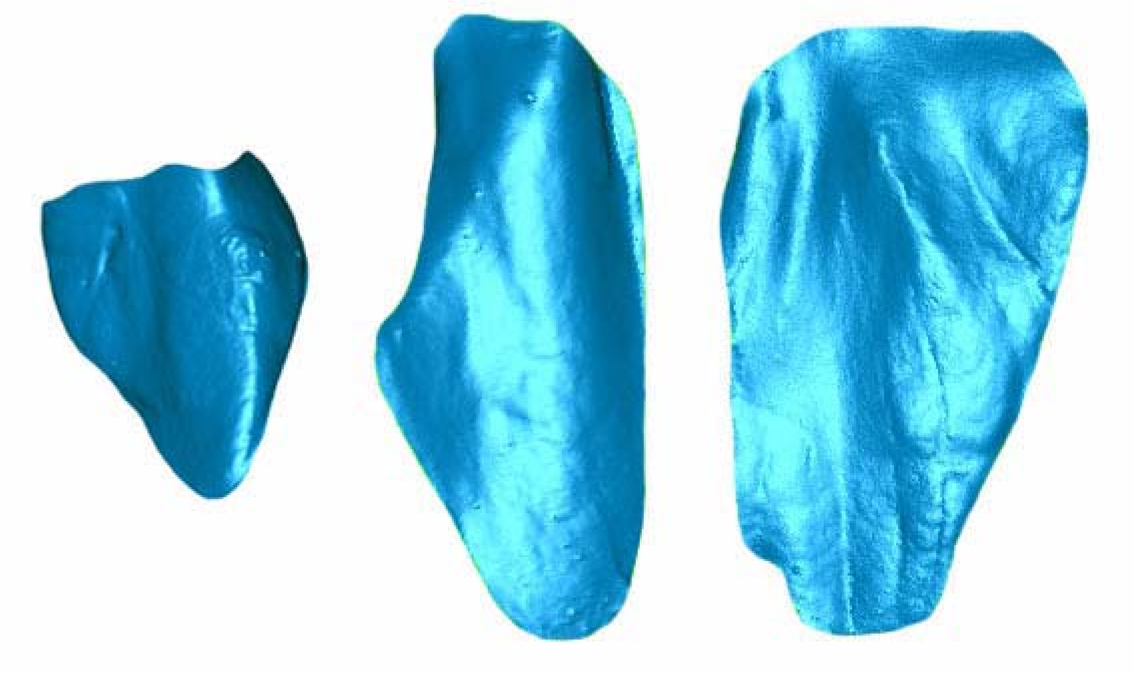

Figura 30. *Escaneados 3D de los moldes realizados de las tres fosas de la escápula (de izquierda a derecha: fosas supraespinosa, infraespinosa y subescapular) de un chimpancé (*Pan troglodytes*).*

El estudio de las áreas 3D de las fosas de la escápula ha demostrado ser un buen estimador del tamaño del músculo (Bello-Hellegouarch *et al*. 2013a). Aunque hasta ahora hemos analizado únicamente la proporción entre las áreas de las fosas supraespinosa e infraespinosa, planeamos incluir la fosa subescapular, situada en la cara anterior de la escápula. La mayoría de estudios que tratan de inferir el uso de la extremidad anterior en relación con el modo de locomoción se han centrado exclusivamente en los músculos de la cara dorsal de la escápula (supraespinoso e infraespinoso), ignorando que la superficie anterior de la escápula está ocupada exclusivamente por el músculo subescapular (Larson & Stern 2013). El músculo subescapular podría influir decisivamente en la forma de la escápula o, al menos, con la misma intensidad que los músculos de la cara dorsal (Larson & Stern 1986, 2013). Por tanto, sería de gran interés realizar un estudio detallado de las áreas de las tres fosas con el fin de conocer la influencia relativa de cada músculo, incluido el subescapular, en la forma de la escápula, y la relación entre los tamaños de las tres fosas y los diferentes tipos de locomoción. Ya hemos escaneado los moldes 3D (*figura 30*) de 253 individuos pertenecientes a diversos grupos locomotores, y disponemos ya de las áreas 3D de la mayoría de ellos.

El análisis detallado de las adaptaciones de la escápula a los modos de locomoción en primates pronógrados sugiere que es prácticamente imposible crear un sistema de clasificación de estos modos de locomoción sin perder parte de la información. Es excepcionalmente problemático realizar con precisión una clasificación de todos los modos de locomoción existentes, ya que los primates son los mamíferos que exhiben mayor diversidad de comportamientos locomotores, combinándolos de un modo tan extremo que difieren no sólo entre subfamilias o géneros (Preuschoft 1989) sino también entre individuos, o incluso en función de las condiciones externas en las que se mueven. Para clasificar la locomoción de las especies analizadas se consideraron los comportamientos locomotores más frecuentes con el fin de simplificar su categorización y su posterior análisis. Sin embargo, muchos de los primates pronógrados estudiados son capaces de realizar comportamientos infrecuentes pero críticos (Prost 1965), esenciales para la obtención de alimento o para escapar, que crean enormes cargas que pueden afectar a la forma de la escápula a pesar de su baja frecuencia (Rose 1973; Martin 1990; Schmidt 2010). Además, se ha sugerido que las funciones no locomotoras de las extremidades anteriores, como la búsqueda de alimento o el *grooming*, podrían tener un fuerte impacto en la anatomía de la extremidad anterior, mayor incluso que las adaptaciones locomotoras (Larson 1998; McGraw 1998; Larson *et al*. 2000; Hanna *et al*. 2006; Stevens 2008; Wright-Fitzgerald *et al*. 2010). Sin embargo, algunos autores han sugerido que las fuerzas transmitidas a través del hombro durante los comportamientos posturales son menores que las transmitidas durante la locomoción, no requiriendo ninguna adaptación especial (Roberts 1974; Rose 1974; Preuschoft *et al*. 2010). Anapol & Gray (2003) han sugerido que estas funciones posturales podrían afectar más a la morfología de la extremidad anterior que a la del hombro. En cualquier caso, aunque nuestros resultados pueden servir de base para análisis más detallados de la morfología de la escápula y sus adaptaciones locomotoras en primates, es necesario definir categorías locomotoras más precisas y realistas con el fin de comprender los requisitos anatómicos y morfológicos precisos de cada modo de locomoción propio de cada taxón.

Finalmente, el análisis de la expresión de las isoformas de la cadena pesada de la miosina en el músculo supraespinoso ha demostrado ser útil para caracterizar las adaptaciones locomotoras de los primates (Potau *et al*. 2011, 2012). Durante las disecciones realizadas en esta Tesis Doctoral se han tomado muestras de todos los músculos del manguito rotador, al igual que de todos los músculos del brazo, antebrazo y mano de las diferentes especies estudiadas. Estas muestras se están procesando en estos momentos con el fin de realizar el mismo tipo de análisis de las miosinas y así poder comprender mejor el funcionamiento de estos músculos en los diferentes grupos locomotores.

“Learn from yesterday, live for today,
hope for tomorrow. The important
thing is to not stop questioning.”

Albert Einstein

III. Conclusiones

Conclusiones metodológicas

- La proporción 3DI, obtenida a partir de los escaneados en 3D de los moldes de las fosas es la proporción más fiable en ausencia de información muscular.
- Hay que ser cautos al hacer inferencias locomotoras exclusivamente a partir de datos osteológicos ya que, aunque se asume que existe una relación directa entre el tamaño de la inserción y el del músculo, son diversos los factores que determinan el tamaño de la inserción muscular.
- La RT-PCR es una técnica que complementa la información obtenida mediante técnicas osteológicas o electromiográficas.

Morfología y función

Cautividad vs Libertad

- No existen diferencias significativas en la morfología de la escápula entre primates hominoideos procedentes de cautividad y de libertad, lo que sugiere que la cautividad no afecta significativamente a su morfología.
- Las escápulas de los especímenes en cautividad analizados se pueden utilizar en análisis morfológicos o taxonómicos, solos o combinados con especímenes en libertad, ya que son representativos de las especies en su conjunto.

Primates ortógrados

- Tanto las metodologías cualitativas (GM) como las cuantitativas (índices S/I) confirman la presencia de diferencias significativas en la morfología de la escápula relacionadas con las adaptaciones locomotoras de los primates hominoideos.
- Las principales diferencias en la forma de la escápula están relacionadas con la proporción entre las fosas supraespinosa e infraespinosa, y con la longitud e inclinación de la espina de la escápula.
- *Homo* y *Pongo* se caracterizan por una fosa supraespinosa relativamente pequeña, relacionada con las adaptaciones a la vida arbórea en *Pongo* y con la necesidad de movimientos rápidos y precisión de los movimientos de la articulación glenohumeral en *Homo*.
- *Pan*, *Gorilla* e *Hylobates* se caracterizan por una fosa supraespinosa relativamente grande, relacionada con la locomoción terrestre en los *knuckle-walkers* (*Pan* y *Gorilla*), y con la braquiación en *Hylobates*.

Primates pronógrados

- La locomoción es el factor que más se correlaciona con la forma de la escápula en primates pronógrados, seguido de la filogenia a nivel de familia.
- Los cuadrúpedos terrestres comparten una fosa supraespinosa relativamente más grande que la de los cuadrúpedos arbóreos, relacionada con la estabilización de la articulación glenohumeral

durante la fase de soporte de la locomoción cuadrúpeda terrestre.

- La suspensión bimanual, el *pronograde clambering* y la suspensión cuadrúpeda tienen escápulas caracterizadas por una fosa infraespinosa relativamente grande, estabilizadora de la articulación glenohumeral.
- El *slow-climbing quadrupedalism* se caracteriza por fosas supraespinosa e infraespinosa relativamente bien desarrolladas, necesarias para la estabilización de la articulación glenohumeral, altamente móvil, y la participación del músculo infraespinoso en movimientos que combinan rotación lateral con abducción de la extremidad.
- Las fosas supraespinosa e infraespinosa de los *leapers* están relativamente bien desarrolladas para estabilizar su articulación glenohumeral, permitiendo el aumento del momento de inercia de la extremidad anterior durante el *leap*.
- Los *vertical clingers and leapers* no emplean las extremidades anteriores directamente en el desplazamiento, por lo que sus escápulas son largas y estrechas, con fosas supraespinosa e infraespinosa reducidas, de modo que la capacidad de aducción y abducción es reducida.
- La escápula de los *vertical clingers* se caracteriza por fosas supraespinosa e infraespinosa poco desarrolladas, pero con una gran área de inserción del músculo redondo mayor, importante en la aducción del húmero durante el *climbing* y el *clinging*.

Miosinas y función

- Las diferencias funcionales del músculo supraespinoso entre los primates pronógrados y ortógrados se reflejan en los patrones de expresión de las isoformas de la cadena pesada de las miosinas (MHC).
- Ninguno de los primates pronógrados expresa la isoforma MHC-IIx, la más rápida y menos resistente, en el músculo supraespinoso, lo que pone de relieve la importancia del músculo supraespinoso como un músculo postural (estabilizador de la articulación glenohumeral).
- El músculo supraespinoso de los primates ortógrados, incluidos los humanos, muestra una mayor expresión de las dos isoformas rápidas MHC-II, típica de músculos rápidos y potentes con poca resistencia a la fatiga, lo que pone en evidencia la función elevadora del músculo supraespinoso en los primates ortógrados.
- Aunque los primates ortógrados no humanos emplean varios modos de locomoción (braquiación, *arm-swinging*, *knuckle-walking*), no se observan diferencias significativas en los patrones de expresión de las isoformas de MHC en relación con sus modos de locomoción.
- Los humanos modernos presentan un mayor porcentaje de expresión de la isoforma rápida MHC-IIx en comparación con los primates ortógrados que puede deberse a la gran movilidad y precisión de los músculos de la extremidad anterior cuya función locomotora ha sido reemplazada por una función manipulativa.

“If I have seen further it is by standing on the shoulders of Giants.”

Isaac Newton

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"Science is the poetry of reality"

Richard Dawkins

V. Publicaciones

1. The rotator cuff muscles in Hominoidea: evolution and adaptations to different types of locomotion.

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RESUMEN

Los músculos del manguito rotador (subescapular, supraespinoso, infraespinoso y redondo menor) juegan un papel fundamental en el movimiento y estabilización de la articulación glenohumeral en los primates, proporcionándole la movilidad necesaria para el desplazamiento, pero manteniendo al mismo tiempo la estabilización necesaria (Ashton & Oxnard 1963; Roberts 1974; Larson & Stern 1986, 1987).

El músculo supraespinoso estabiliza la articulación glenohumeral en posturas cuadrúpedas, en la fase de soporte de la locomoción cuadrúpeda, y durante la fase inicial de la elevación de la mano. Además, es esencial como músculo abductor (junto con el deltoides) durante la elevación de la extremidad anterior (Larson & Stern 1986, 1987, 1989).

El músculo infraespinoso es principalmente un rotador lateral de la extremidad anterior. Además, estabiliza la articulación glenohumeral en posturas cuadrúpedas y durante la fase de soporte de la locomoción cuadrúpeda, al igual que durante la fase de soporte del *arm-swinging* (Larson & Stern 1986, 1987). Por este motivo, este músculo es relativamente grande en primates con comportamientos locomotores arbóreos.

El músculo redondo menor es un rotador lateral del húmero, y también participa en el mantenimiento de la posición de la cabeza del húmero en la cavidad glenoidea (Larson & Stern 1986; Aiello & Dean 1990).

El músculo subescapular presenta tres partes funcionalmente diferenciadas, de modo que actúa como rotador medial de la extremidad anterior; rotación que puede combinarse con abducción (por la porción superior del músculo) o aducción (por la porción inferior del músculo) dependiendo de la posición y los movimientos de la extremidad (Larson & Stern 1986; Larson 1988).

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Chapter III

The Rotator Cuff Muscles in Hominoidea: Evolution and Adaptations to Different Types of Locomotion

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Abstract

The rotator cuff muscles (subscapularis, supraspinatus, infraspinatus and teres minor) are the principal stabilizers of the glenohumeral joint in primates. This function is particularly important in hominoids due to their orthograde corporal pattern, characterized by a dorsal position of the scapulae, a high mobility of the glenohumeral joint and the presence of tensile forces that affect the shoulder region during locomotion. These functional and physiological conditions imply an special morphology of the rotator cuff muscles in hominoids, which present an increased global mass and important differences in the proportion of the different muscles with respect to the more quadrupedal pronograde primates. Although sharing some similarities, the different general that form the Hominoidea have developed different types of locomotion such as brachiation (*Hylobates*), arm-swinging and vertical climbing (*Pongo*), knuckle-walking (*Gorilla* and *Pan*) and bipedalism (*Homo*). Thus, the morphology of the rotator cuff muscles in these genera is also related to the functional requirements of these types of locomotion. In this chapter we will discuss the anatomical and functional aspects of the rotator cuff muscles in hominoids by focusing on the evolutionary transformations and adaptations related to the different locomotor modes developed by hylobatids, orangutans, gorillas, chimpanzees and modern humans.

Introduction

As stressed by Gebo (2010: p. 530), "life in the canopy is a constant stream of body adjustments". Environmental changes result in the alteration of the requirements for posture and locomotion, requirements that are reflected in anatomical adaptations (Sonnabend and Young, 2009), closely related to the type of locomotion used to move through the canopy.

It has been proposed that hominoids became different from other primates (and from mammals in general) due to their specific adaptations to an arboreal environment where the capacity to a below-branch forelimb-dominated arboreal locomotion was an advantage in survival (Le Gros Clark, 1959; Larson, 1993; Fleagle, 1999; Sonnabend and Young, 2009). Thus, extant apes are characterized by some locomotor specializations, sharing body morphologies associated to their locomotor behaviors (Ward, 2007), especially those related to suspension and orthograde climbing, many of them still seen in modern humans. Crucial anatomical features characterizing the Hominoidea are seen in the thoracic region and principally the shoulder, which displays a significant amount of morphological variation related to an accommodation to different habits and habitats (Figure 1; Oxnard, 1967; Larson, 1993). Pronograde primates (and mammals in general) share a pronograde back, a deep dorso-ventrally thorax, a scapula located in the parasagittal plane lateral to the rib cage and a glenohumeral joint adapted for quadrupedal locomotion (both arboreal and terrestrial) with movements restricted to the parasagittal plane (Schultz, 1930; Roberts, 1974; Aiello and Dean, 1990; Larson, 1993;

Sonnabend and Young, 2009; Gebo, 2010). In contrast, living ape and human backs are adapted to vertical and erect postures, sharing an erect back (what is commonly known as orthogrady) and a thorax that is shallow antero-posteriorly and wide laterally. Their scapula is displaced to a dorsal position rather than along the side of the ribcage as in quadrupedal primates, forcing the shoulder to the sides and away from the midline of the body, developing a more mobile and less stable glenohumeral joint with the glenoid fossa facing laterally rather than ventrally, which can additionally rotate and move in the coronal plane, allowing more freedom of mobility with multi-directional movements (the shoulder joint is the most freely movable in the body of hominoids; Figure 1; Keith, 1923; Schultz, 1930; Roberts, 1974; Aiello and Dean, 1990; Larson, 1993; Fleagle, 1999; Sonnabend and Young, 2009; Gebo, 2010). The shoulder acquired the required mobility to reach the irregular supports of a discontinuous arboreal substrate (Larson, 1993), allowing more specialized forms of locomotion, including brachiation, vertical climbing, suspensory posture and knuckle-walking, and, in modern humans, the use of the hand for complex manipulation (Schultz, 1961; Corruccini and Ciochon, 1976; Aiello and Dean, 1990; Larson, 1993; Sonnabend and Young, 2009). However, it should be noted that the increase of mobility reduces the stability of the glenohumeral joint (Roberts, 1974; Larson, 1993); this means that the shoulder region will reflect a compromise between the free mobility demands and the need for stability, facing the disruptive forces generated during locomotion and the support of the body weight (Larson, 1993).

Within extant apes, hylobatids are the more arboreal ones, being true brachiators due to their particular type of locomotion where the arms are usually fully extended above their head in order to suspend and propel the body through the trees (Napier, 1963; Tuttle, 1975; Fleagle, 1999). Gorillas, chimpanzees and orangutans are considered modified brachiators (Aiello and Dean, 1990) because they use their lower limbs too to a greater or lesser extent in order to provide some support for the body. Orangutans, as hylobatids, almost never move on the ground, but they differ in that the former show a larger body size, moving cautiously through the upper levels of the canopy with quadrumanous climbing and arm-hanging (Fleagle, 1999; Thorpe and Crompton, 2005, 2006; Ward, 2007). Common chimpanzees are arboreal especially when they forage, hunt and sleep, but, in contrast to orangutans, they spend much of their time as terrestrial knuckle-walkers (Goodall, 1965; Fleagle, 1999). The locomotor behavior of bonobos is less well studied, but it seems to be somewhat similar to that of common chimpanzees (Doran, 1993), although it is thought (Susman, 1984; Doran and Hunt, 1994) that bonobos often engage in more arboreal leaping, diving and arm-swinging. Gorillas are the biggest modern primates and are almost exclusively terrestrial, although sporadically in certain habitats they climb trees, frequently for feeding and sleeping (Tuttle and Watts, 1985; Remis, 1995; Fleagle, 1999). Knuckle-walking, the primary type of locomotion of the African apes, is a quadrupedalism that has been secondarily imposed on a forelimb that was being primarily adapted to suspensory postures and locomotion (Larson and Stern, 1987). Thereby, gorillas and chimpanzees may have evolved to acquire those functions related to quadrupedal weight bearing, but without losing the previous arm-swinging and suspensory functions (Oxnard, 1969). Modern humans, with their bipedal locomotion, lost any adaptations needed solely for locomotion, accentuating those ones that permitted them to transform the upper limb into an almost exclusively manipulative extremity possessing important tactile, prehensile, manipulatory, communicative and agonistic functions (Ziegler, 1964; Oxnard, 1969; Fleagle, 1999).

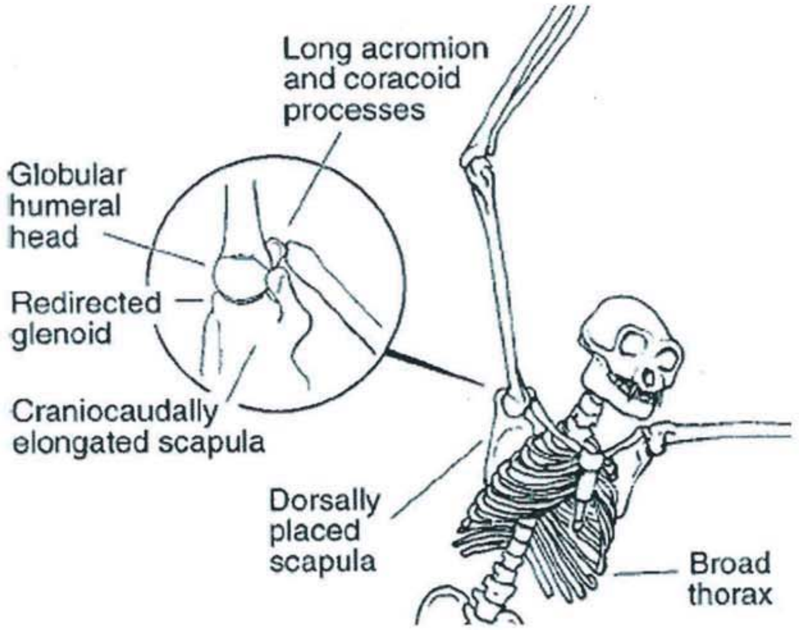

Figure 1. Characteristic skeletal features of the shoulder region of extant apes (modified from Fleagle, 1999).

The comparative morphology of the primate upper limb, and more specifically, of the scapula, has been very useful to establish functional differences in behaviour among hominoids (Ashton and Oxnard, 1964; Roberts, 1974; Corruccini and Ciochon, 1976). This focus on the primate scapula is due to the fact that this is the most variable bone of the forelimb (Oxnard, 1967), and, as it is suspended almost completely by muscles it is supposed to reflect, at least in some of its variations, the deep relationship with the function of the upper limb (Figure 2; Inman *et al*, 1944; Oxnard, 1967) and the forces this limb has to endure during locomotor behaviors. For example, the shoulder of brachiators is mainly subject to tensile forces, while the shoulder of quadrupeds is mainly subject to compressive forces (Oxnard, 1967, 1969; Roberts, 1974; Larson, 1993).

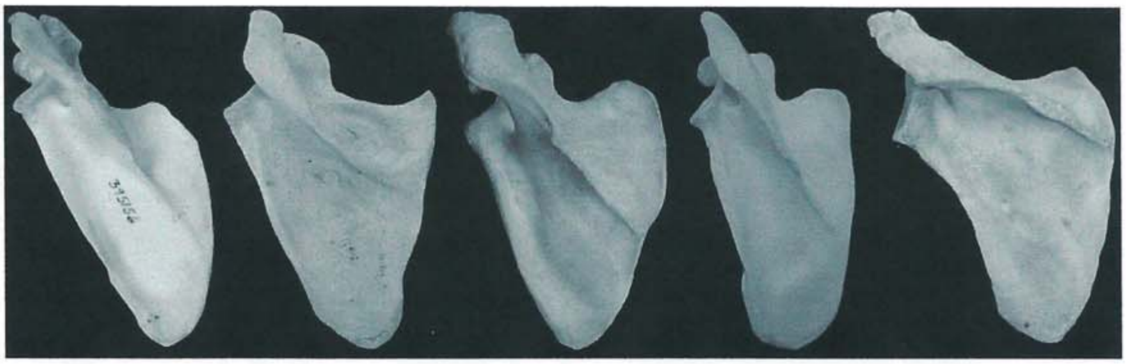

Figure 2. Scapulae of the different groups of the Hominoidea. From left to right: *Hylobates* (ref.395156, from the Royal Belgian Institute of Natural Sciences), *Pongo* (ref.94-0703 from the Natural History Museum of Barcelona), *Gorilla* (ref.2003-0544 from the Natural History Museum of Barcelona), *Pan* (ref.95.0258 from the Natural History Museum of Barcelona) and *Homo* (ref.038 from the Unit of Human Anatomy and Embryology of the University of Barcelona).

Before presenting our own data and describing in detail the differences between the shoulder, and more specifically the scapula and scapulohumeral muscles of the different hominoid taxa, it is convenient to carry out a brief, simplified introduction to some of the muscles attached onto the scapula.

Brief Introduction to the Rotator Cuff Muscles

As we explained above, the emphasis on the mobility of the hominoid shoulder joint results in a reduction of the stability of the joint (Roberts, 1974; Larson, 1993), thus requiring additional stabilization to prevent its dislocation. This is easy to understand when we observe the bony architecture of the glenohumeral joint, with its large articulating humeral head and its relatively small glenoid surface (Terry *et al*, 2000). This stabilization is especially important during behaviors that imply large tensile stress in the joint, so it is not maintained solely by static osseoligamentous structures but also, and principally, by dynamic stabilizers (Larson and Stern, 1986; Terry *et al*, 2000; Jenkins, 2009). The dynamic stabilization is accomplished by a group of muscles known as the rotator cuff or the musculotendinous cuff of the shoulder (Hess, 2000; Jenkins, 2009), whose tendons are closely related to the capsule of the joint anteriorly, above and posteriorly (Terry *et al*, 2000; Jenkins, 2009). Anteriorly, the cuff is made up of the subscapularis muscle (Figure 3), while posteriorly, from a superior to an inferior position, it is made up of the supraspinatus, infraspinatus and teres minor muscles (Figure 4).

The supraspinatus muscle originates from the dorsal surface of the scapula above the spine, known as supraspinous fossa, and from the fascia covering the muscle itself (Figure 4). It passes first over the top of the glenohumeral joint, inserting on the proximal part of the great tubercle (Ashton and Oxnard, 1963; Jenkins, 2009). Before its insertion, the fibers converge upon a short and stout tendon that adheres to the glenohumeral capsule. Between the supraspinatus and the acromion we find the subacromial bursa. The supraspinatus is principally an abductor of the arm, assisting the deltoid in this movement (Larson and Stern, 1986; Aiello and Dean, 1990; Jenkins, 2009), and it is also important to resist humeral displacement (Larson and Stern, 1986, 1987).

The infraspinatus muscle originates from the infraspinous fossa and from its covering fascia, and inserts on the dorsal facet of the great tubercle, inferiorly to the the supraspinatus insertion (Figure 4). The teres minor originates from about the upper two thirds of the posterior surface of the lateral border of the scapula, and from a septa between it and both the infraspinatus above and the teres major below (Figure 4). This muscle inserts distally on the greater tubercle, directly inferior to the insertion of the infraspinatus, after adhering to the dorsal aspect of the glenohumeral capsule. Both the teres minor and the infraspinatus are primarily lateral rotators of the humerus, and they also participate in the maintenance of the position of the humeral head during other movements of the arm (Ashton and Oxnard, 1963; Larson and Stern, 1986; Aiello and Dean, 1990; Jenkins, 2009).

The subscapularis muscle originates from most of the anterior surface of the scapula, known as subscapular fossa, and passes across the front of the glenohumeral joint to its insertion on the lesser tubercle of the humerus (Figure 3). Before inserting, the fibers converge upon a short and thick tendon which adheres to the anterior part of the glenohumeral capsule (Ashton and Oxnard, 1963). Between this muscle and the neck of the scapula lies the subscapularis bursa, usually opening into the synovial cavity of the glenohumeral joint. The subscapularis muscle produces mainly medial rotation, as well as protection to prevent anterior dislocation of the head of the humerus (Aiello and Dean, 1990; Jenkins, 2009).

Figure 3. Anterior view of the dissection of *Pan troglodytes* showing the anterior side of the rotator cuff muscles and some other muscles of the shoulder and arm. 1: Subscapularis. 2: Teres major. 3: Coracobrachialis. 4: Biceps brachii (caput breve).

Figure 4. Dorsal view of the dissection of a male *Pan troglodytes* showing the dorsal side of the rotator cuff muscles and some other muscles of the shoulder and arm. 1: Supraspinatus. 2: Infraspinatus. 3: Teres minor. 4: Teres major. 5: Triceps brachii (caput longum).

Thus, in general, the rotator cuff contributes, on the one hand, to the mobility of the shoulder, and on the other hand, to the dynamic stabilization of the shoulder (Roberts, 1974; Sonnabend and Young, 2009), by holding the head of the humerus in the glenoid cavity with a dynamic steering mechanism (Terry *et al*, 2000; Jenkins, 2009).

Accordingly, the architectural arrangement of the rotator cuff muscles fibers is consistent with this stabilizing role, as they seem to be configurated for force production rather than excursion (Ward *et al*, 2006).

Since this increasing need for stability seems to be related to the increased range of motion of the glenohumeral joint, i.e. to the increased use of the arm away from the sagittal plane (Sonnabend and Young, 2009), it seems logical to think that the appearance of a true rotator cuff, with tendons closely related to the capsule and to each other, should be associated with the ability to carry out regular overhead activity.

Indeed, some authors (e.g. Sonnabend and Young, 2009) consider that only primates with an important amount of arboreal locomotion develop true rotator cuff, such as hominoids and some arboreal New World monkeys.

As we will be seen throughout this chapter, the evolution of the bony skeleton of the shoulder girdle has been well described, specially the morphology of the scapula, while there is little information related to the soft tissue, and in particular to the rotator cuff (Sonnabend and Young, 2009).

Many of the measures and studies related with the scapula are not focused on the rotator cuff mechanism, that is, many authors employ some anatomical measures only in order to discriminate between, for example, locomotor groups, without focusing on where the differences are, or which is the reason (related to the musculature) for those differences.

However, as we shall see later, in the last years the musculature *per se* is starting to be the subject of more studies, including gross anatomical, electromyographic and myosine analyses.

Below we will thus provide a detailed review of what is currently known about the rotator cuff muscles in hominoids, based on our own studies and on those of other authors, including classical methods such as the analysis of linear measures of the scapula to the most innovative techniques such as 3D geometric morphometrics and the analysis of the expression of the myosin heavy chain (MHC) isoform.

State of the Art Concerning the Rotator Cuff Muscles

After several empirical studies, from the removal of muscles in rats (e.g. Wolffson, 1950) to genetically modified mice (e.g. Green *et al*, 2011), it has been clearly demonstrated that the rotator cuff muscles have a significant influence on the scapular shape (Howell, 1917; Wolffson, 1950; Roberts, 1974; Green *et al*, 2011), enlarging or reducing their relative sizes and generating stresses that have a great impact in the scapular structure (Inman *et al*, 1944; Roberts, 1974). Thus, the adaptations of size, shape and position of the muscles according to the functional demands of the upper limb can cause adaptations in the position and orientation of the insertions on the bones and joints over which the muscles act, increasing the mechanical efficiency of arm-raising, compared to quadrupeds (Inman *et al*, 1944; Roberts, 1974; Ashton and Oxnard, 1964; Oxnard, 1967). This relationship between the scapular shape and the muscular features of the rotator cuff justifies that the scapula is usually studied in order to obtain muscular information from the osteological data, an easier way to research, due to the limitations (or impossibility in the case of extinct species) related to the direct study of the muscles (principally, the difficulty in obtaining cadavers of primates).

In relation to the rotator cuff mechanism, the model proposed by Inman *et al* (1944) was assumed to be correct and most of the scapular shape variables employed in several studies were derived from this model (see, e.g. Ashton & Oxnard, 1963). According to this model in modern humans there is a force couple operating at the glenohumeral joint, the upper unit of the model being composed by the deltoid and supraspinatus, the lower unit including the infraspinatus, teres minor and subscapularis; the pressure and friction of the humeral head at the glenoid was also taken into account. According to Inman, the deltoid, assisted by the supraspinatus, provides the power to elevate the arm, while the lower unit acts collectively to hold the humeral head down thus preventing the tendency for the deltoid to produce superior humeral displacement. This model was considered correct for many years, not only for modern humans, but for the great apes (Tuttle and Basmajian, 1978a, 1978b), implying that the glenohumeral joint integrity was maintained solely by osseoligamentous structures (Tuttle and Basmajian, 1978a, 1978b). However, further EMG analyses of non-human primate shoulder muscle function (Larson and Stern 1986, 1987) have shown that this model of force couple is not correct in at least chimpanzees, and probably also in other hominoids, beause these analyses emphasized the distinct role of each member of the rotator cuff in free arm movements (Larson and Stern, 1986). Furthermore, the rotator cuff has a second and equally important function in stabilizing the shoulder joint, a role proposed by Roberts in 1974. Therefore, considering that each muscle plays a distinct role in the rotator cuff mechanism for the free movement of the arm, we will try to make its understanding clear and simple, by examining separately each of the rotator cuff muscles.

Supraspinatus

The supraspinatus is the better studied of the rotator cuff muscles, probably due to its importance in stabilizing the joint, in abducting the arm, and also because of its clinical implications (e.g. the subacromial impingement, a typical human disease, see Potau *et al*, 2007). As explained above, most of the studies of the rotator cuff muscles are based on the analysis of the shape and size of their origins, especially in the case of the supraspinatus and the infraspinatus muscles. Thus, much of the information available concerns the supraspinous and infraspinous fossae, obtained in different ways, e.g. multivariate analyses of lineal measures (Ashton and Oxnard, 1964; Ashton, Oxnard and Spence, 1965; Oxnard, 1967; Oxnard and Neely, 1969; Roberts, 1974) and geometric morphometric analyses of the scapula (Young, 2002, 2008). This is a useful way to obtain information about a muscle when this muscle is absent (e.g. fossils; osteological collections), but one must be cautious because our own studies indicate that the size of the muscle and of its origin (in this case, the fossae of the scapula) may not be as closely related as previously though (Bello-Hellegouarch *et al*, unpublished data).

It is clear that the morphology of the supraspinatus varies with the type of locomotion. Hominoids are associated with relatively well-developed supraspinous fossa (Frey, 1923; Schultz, 1930; Inman *et al*, 1944; Roberts, 1974; Corruccini and Ciochon, 1976; Shea, 1986; Larson, 1993), and, by implication, with well developed supraspinatus muscles. This seems to be associated to the presence of relatively large, heavy and powerful limbs with a great need for glenohumeral joint stabilization during the elevation of the upper limb (Roberts, 1974; Corruccini and Ciochon, 1976; Larson and Stern, 1986; Larson, 1993). While in African apes the supraspinatus is relatively broader, especially in gorillas (Schultz, 1930; Inman *et al*, 1944; Raven, 1950; Roberts, 1974), in orangutans and modern humans the proportions of the supraspinatus are only slightly larger than those seen in quadrupeds, i.e. the muscle is long and narrow compared to the infraspinatus (Ashton and Oxnard, 1963).

Electromyographic analyses provided additional information confirming a great part of the conclusions that were previously obtained from osteological data (Inman *et al*, 1944; Jungers and Stern, 1984; Tuttle and Basmajian, 1978a, 1978b; Larson and Stern, 1986, 1987), as well analyses done on the muscular weights (Potau *et al*, 2009). In general, the supraspinatus seems to play a similar role in different species of primates, depending on their locomotor behaviors. That is, the supraspinatus is extremely important in quadrupedal postures and locomotor support phases, as it stabilizes the glenohumeral joint; it plays a major role assisting the deltoid during the abduction of the upper limb in free arm movements; and it may also occasionally make a small contribution during the swing phase of the quadrupedal locomotion (Larson and Stern, 1986, 1987; Larson, 1989).

The knuckle-walkers are the hominoids that possess relatively broader scapulae and large supraspinous fossae, i.e. gorillas and chimpanzees (and a large infraspinous fossa, as we shall see later; Schultz, 1930, Roberts, 1974; Aiello and Dean, 1990; Potau *et al*, 2007; Young, 2008). In *Gorilla*, the most highly adapted hominoid for quadrupedalism, the supraspinous fossa is relatively larger than in other primate species; this can be explained because these apes need a greater stabilization due to their extremely large body size and the compressive forces that they have to bear since they use the upper limb in an abducted and externally rotated position during feeding (Roberts, 1974; Taylor and Slice, 2005; Potau *et al*, 2007). This has been confirmed by electromyographic studies that showed that during knuckle-walking, the supraspinatus, together with the infraspinatus, are essential stabilizers of the glenohumeral joint, which undergoes severe shearing stress, controlling specifically the humeral retraction during the support phase (Roberts, 1974; Tuttle and Basmajian, 1978b; Larson and Stern, 1987; Larson and Stern, 1992). During the first part of the swing-phase of the arm-rising the supraspinatus is recruited in concert with the deltoid muscle to abduct the upper limb in hominoids (Inman *et al*, 1944; Tuttle and Basmajian, 1978a; Larson and Stern, 1986; Larson and Stern, 1989). This is especially important during brachiation, vertical climbing and suspensory locomotion (Inman *et al*, 1944; Oxnard, 1966, 1967; Ashton and Oxnard, 1964; Ciochon and Corruccini, 1977). Apart its role as abductor, the supraspinatus, with its attachment on the top of the great tubercle, bears the main responsibility for preventing the superior displacement of the humeral head provoked by the deltoid and for stabilizing the humerus during the initial phase of brachial elevation (Howell *et al*, 1986; Larson and Stern, 1986; Thompson *et al*, 1996). Once the initial phase of brachial elevation passes, the tendency of the deltoid to displace the humerus decreases, and then the supraspinatus acts to assist the deltoid in the abduction (Larson and Stern, 1986).

In orangutans the supraspinous fossa may seem poorly developed due to the broad infraspinous, but it is, in fact, better developed than in any pronograde primate (Roberts, 1974) although it is quite small if compared to the African apes (Oxnard, 1984; Young, 2002). This supraspinous fossa, combined with the relatively large infraspinous fossa, may reflect the great range of circumduction that the orangutan can display when it has the forelimb raised above the shoulder level, being necessary a much greater muscular force to secure the shoulder joint (Roberts, 1974). However the especial locomotor behaviour of orangutans is reflected in a scapula that shares some similarities with that of the ateline monkey *Lagothrix* (Young, 2003) and of other arboreal quadruped primates, as will be seen below. Hylobatids are different from the great apes because they have a relatively small supraspinous fossa (and, as we shall see later, a relatively small infraspinous fossa), a difference that can reflect the overwhelming lineage-specific specializations of their shoulder for brachiation (Young, 2008). Hylobatid dissimilarities to the great apes, and the specialized nature of their locomotion, i.e., a true brachiation, are considered by some authors to reflect specialized and divergent adaptations; so, the great apes are more likely to reflect the ancestral morphotype, being less specialized than hylobatids (Young, 2003). In modern humans the habitual use of the arm below the level of the shoulder and the fact that the forelimb has mainly manipulative skills, reduced the levels of shearing stress in the joint and thus the need for a developed supraspinatus muscle, being the supraspinous fossa as well as the rest of the rotator cuff muscles relatively poorly developed (Roberts, 1974; Potau *et al*, 2007). This reduction of the rotator cuff is beneficial for modern humans as it provides to the glenohumeral joint greater speed and precision on its movements, which is essential to the manipulative skills of the modern human upper limb (Potau *et al*, 2007). Electromyographic analyses of modern humans confirm that the supraspinatus acts together with the deltoid to abduct the arm (Inman *et al*, 1944). Thus, we find in humans a unique arrangement of the shoulder muscles. Some of their features are similar to those of apes, e.g. their extremely huge deltoid, while others resemble those of quadrupeds, e.g. the reduction of the development of the rotator cuff muscles. This particular mosaic distribution allows modern humans to raise the arm as freely as that of apes, but without their power, duration and frequency (Ashton and Oxnard, 1963, 1964; Oxnard, 1967, 1969; Larson, 1993). Few studies have examined the molecular characteristics of the rotator cuff muscles, and the few ones that were performed were related to the quantification and distribution of the muscular fibers (Singh *et al*, 2002; Schmidt and Schilling, 2007). Recently, we started to examine the mRNA expression of the different MHC (myosin heavy chain) isoforms of the rotator cuff muscles (Potau *et al*, 2011). Three different MHC isoforms can be found in the skeletal muscles of adult mammals, and their expression is related to the functional properties of the muscle fibres (Bottinelli and Reggiani, 2000). Those isoforms are the slow MHC-I, the fast MHC-IIa and the fastest MHC-IIx. A fourth isoform is expressed only in very small mammals, the MHC-IIb (Baldwin and Haddad, 2001). In general, the slow postural muscles express mainly the slow MHC-I isoform, with a variable expression of the MHC-IIa isoform (Fitts *et al*, 1991; Baldwin, 1996; Fitts and Widrick, 1996; Schiaffino and Reggiani, 1996; Rivero *et al*, 1999; Talmadge, 2000). Furthermore, in the powerful, fast, and less resistant muscles all three isoforms can be expressed in variable proportions, but with a predominance of the MHC-II isoforms (Harridge *et al*, 1998; Larsson and Moss, 1993). While pronograde primates show higher proportions of the slow and resistant MHC-I isoform, evidencing the importance of their supraspinatus as a postural muscle, hominoids show higher proportions of the two fast MHC-II isoforms than the slow MHC-I isoform, a typical expression of fast and powerful muscles, with low resistance to fatigue (Klitgaard *et al*, 1990; Harridge *et al*, 1996). This is an evidence for the elevator function of the supraspinatus in hominoids (Potau *et al*, 2011), as we have seen above. In addition, modern humans showed a higher expression of the fastest MHC-IIx than the rest of hominoids, which can be the result of the greater mobility and precision of the muscles of the arm to perform their manipulative function (Potau *et al*, 2011). We have to point out that, probably due to the small sample size, no differences were found within the expression patterns of the MHC isoforms of the different hominoids. Thus, our studies confirm that molecular techniques can effectively be useful to better understand the different locomotor behaviors displayed by primates.

Infraspinatus

As in the case of the supraspinatous fossa, the predominantly arboreal hominoids share a scapula with relatively broad infraspinous fossa (Frey, 1923; Schultz, 1930; Inman *et al*, 1944; Roberts, 1974; Corruccini and

Ciochon, 1976; Manaster, 1979; Shea, 1986; Larson, 1993). Within hominoids, African apes show the relatively broader infraspinous fossa, gorillas having a relatively broader infraspinous fossae than chimpanzee; this may be a reflection of the greater need for shoulder joint stabilization in gorillas (Schultz, 1930; Roberts, 1974; Corruccini and Ciochon, 1976; Larson, 1993). This is also in agreement with the conclusions obtained from analyses of the muscular weights (Potau *et al*, 2009) and from electromyographic analyses (Tuttle and Basmajian, 1978a, 1978b; Larson and Stern, 1987). During knuckle-walking, highly mobile forelimbs experience greater demands for a different type of glenohumeral joint stabilization, because the shoulder joint bears stress produced by the lateral orientation of the glenoid, resulting in a tendency of the humerus to be displaced dorsally (Roberts, 1974; Larson and Stern, 1987). Such a stabilization seems to be performed by the supraspinatus and the infraspinatus without the assistance of the other muscles of the rotator cuff (Tuttle and Basmajian, 1978b; Larson and Stern, 1987).

During pendant suspension and support phase of arm-swinging, the infraspinatus seems to play a special role in the stabilization of the glenohumeral joint, resisting transarticular stresses suffered by the shoulder joint providing the required humeral head depressor action, although other muscles may also contribute to maintain the joint integrity (Roberts, 1974; Larson and Stern, 1986). In addition, in motions combining abduction with lateral rotation (e.g. overhead reaches) the infraspinatus seems to act as the primary synergist of the deltoid (Larson and Stern, 1986; Larson, 1987), a role that can be explained by the superolateral orientation of the infraspinatus insertion facet on the greater tubercle of the humerus, instead of the more typical lateral orientation usually seen in pronograde primates (Larson and Stern, 1986; Larson, 1995). It therefore seems that the orientation and position of the infraspinatus insertion facet may be a useful indicator of the frequency of arm-raising and overhead forelimb postures (Larson, 1995): within hominoids, hylobatids display highly suspensory behaviors and have the more superolateral oriented facets, orangutans being in an intermediate position, and African apes and modern humans exhibiting the least superolateral oriented facets (Larson, 1995).

The infraspinous fossa of orangutans confirms the important role of the infraspinatus muscle in suspensory locomotion. Orangutans have a broad infraspinous fossa, i.e. in comparison to this fossa the supraspinous fossa appears to be poorly developed (Roberts, 1974). This broad infraspinous fossa is related to the quadrumanous climbing behavior of these Asian apes, and to the greater muscular force required to stabilize the glenohumeral joint while raising the forelimb above their heads (Roberts, 1974). The scapula of hylobatids differs from that of orangutans because the former exhibit a relatively narrower infraspinous fossa (probably related to their overwhelming specializations for true brachiation; see above). This difference can seem to be surprising due to the apparent similar locomotor behavior shared by Asian apes, but when one looks in detail to their behaviors one can see that the scapula of orangutans exhibits a mosaic of suspensory and quadrupedal features, being more closely related to arboreal quadrupeds despite their highly arboreal and suspensory behaviors (Young, 2008). Orangutans are much bigger than gibbons, and this is a crucial difference because they need to avoid lifting their body weight and thus combine both pronograde/orthograde suspensory locomotion and postures that require additional stabilization (Roberts, 1974; Young, 2008). It can thus be said that their principal type of locomotion is moving through the canopy using a slow, cautious pronograde suspension, with frequent "drop leaps" (Thorpe and Crompton, 2005; 2006). Another difference between hylobatids and orangutans concerns the orientation of the base of the scapular spine (Larson and Stern, 1986; Larson, 1995), a feature that seems to have a great influence in the line of action of the infraspinatus as a stabilizer during pendant suspension and the support phase of the arm-swinging. While hylobatids possess extremely acute angles, orangutans display very obtuse scapular spine angles (Larson, 1995), reflecting the different locomotor demands of these taxa.

In modern humans the infraspinatus seemingly participates in the regulation of a typical pendant position of the upper limb. Modern humans have a relatively wide infraspinous fossa (together with a relatively small supraspinous fossa; Roberts, 1974; Aiello and Dean, 1990) and have a nearly horizontal scapular spine, falling outside the range of all other primates; these features are related to the exclusive use of the forelimb as a manipulatory organ (Larson, 1995).

Subscapularis

During primate evolution the subscapularis has reduced its size, being the largest muscle of the rotator cuff in 'lower' primates and decreasing relatively, but only slightly, from phylogenetically plesiomorphic hominoids to modern humans (Inman *et al*, 1944). However, there was an evolutionary increase of the number of fascicules with the expansion of its origin, as well as an increase of the elongation of the scapula (this same skeletal change increased the infraspinous fossa; Inman *et al*, 1944; De Palma, 2008). The subscapularis displays internal functional differentiation, in terms of fiber orientation and origin from different regions of the subscapularis fossa (Larson and Stern, 1986). In the case better studied by Larson and Stern (1986, 1987), the chimpanzees, three different parts are distinguished, and similar structures seem to be found in the other hominoids: there is an upper portion arising in the upper region of the subscapularis muscle, approximately opposite to the supraspinous fossa; the middle portion arises opposite to the infraspinous fossa, but in the anterior side of the scapula; and the lower portion arises from the ventral sulcus, lateral to the axillary bar, and from a common fascial plane with the teres major muscle (Larson and Stern, 1986). Each differentiated region of the muscle acts individually, depending on arm position, to help controlling the rotator state of the humerus (Larson and Stern, 1986; Larson, 1988). Moreover, there seems to be a relationship between the region of the facet of the lesser tubercle of the humeral head, where the fibers insert, and the function of those specific fibers (Larson, 1995). Thus, the abduction and medial rotation is carried out by those fibers inserting onto the more proximal region of the facet, corresponding to the upper portion of the subscapularis, while the adduction and medial rotation is conducted by those fibers inserting more distally, corresponding to the lower portion of the subscapularis (Larson and Stern, 1986; Larson, 1988; Larson, 1995).

The insertion facets in the lesser tubercle of the humerus are thought to be a useful tool to predict the degree of functional differenciation within the subscapularis (Larson, 1995). Hominoids have the longest and narrowest subscapularis insertion facets, confering a greater degree of versatility of the muscle for influencing the position and motion of the humeral head (Larson, 1995); this is important in order to provide higher mobility to the shoulder joint. In summary, the subscapularis is mainly a medial rotator of the arm, rotation that can be combined with abduction (by the upper portion) or adduction (by the lower portion) depending on the position and movements of the upper limb (Larson and Stern, 1986; Larson, 1988). The medial rotation of the humerus is especially important during knuckle-walking in African apes, as it contributes to stabilize the glenohumeral joint (Tuttle and Basmajian, 1978b; Larson and Stern, 1987), compensating for the shearing force that this joint bears due to the dorsal position of the scapula (Roberts, 1974; Larson, 1993). This is consistent with the results obtained from eletromyographic studies (Tuttle and Basmajian, 1978b; Larson and Stern, 1987) and the proportionally large mass of the subscapularis found in chimpanzees (Inman *et al*, 1944; Potau *et al*, 2009).

During the support phase of the arm-swinging of chimpanzees, the subscapularis has no contribution to joint stabilization (Larson and Stern, 1986; Larson, 1988), demonstrating that the force couple model of Inman *et al* (1944) was wrong (see above). By contrast, this muscle is recruited during the support phase of the arm-swinging in hylobatids (Jungers and Stern, 1984), a difference that can be interpreted as a rotatory function, rather than a stabilizing function, because in hylobatids there is a greater participation in free arm movements than in chimpanzees (Larson, 1988). The most important function of the subscapularis takes place during the support (or "pull-up") phase of vertical climbing, where its role as medial rotator becomes extremely important (Larson and Stern, 1986; Larson, 1988). This is a major difference between the subscapularis and the other rotator cuff muscles, and another evidence of the individuality of these muscles. Climbing species are thus expected to have larger subscapularis muscles (Larson, 1988), associated with an increased enlarging of the lateral expansion of the subscapular fossa beyond the ventral bar (the area corresponding to the origin of the lower subscapularis; Larson, 1988; Larson, 1995; Larson and Stern, 1986).

As predicted, great apes show a relatively wider lateral expansion of the subscapular fossa, but not as wide as that found in hylobatids (Larson, 1995). This greater contribution of the subscapularis to the shoulder motion in hylobatids is related to the low degree of humeral head torsion, and the resulting "lateral set" to the gibbon's elbow joint (Larson, 1988), considered an adaptive advantage for limb positioning during brachiation. The "lateral set" refers to the posture of the limbs that these animals adopt while they are resting, with the long axis of the humeral head perpendicular to the glenoid fossa, and the elbow joint in a position such as the arm seems to be laterally rotated, with their forearms splayed out to the side (Larson, 1988). In other words, it is the elbow that is rotated, and not the head of the humerus as it may seem at first sight. The increased demands on the susbcapularis can be explained to overcome the "lateral set", that is, the lateral rotation at the elbow, during free arm movements by the medial rotation of the muscle (Larson, 1995), in order to reestablish the correct arm position needed for normal reaching motions (Larson, 1988). The limited humeral torsion seen in hylobatids can be a compromise between the need to maintain a transverse axis at the elbow joint, which is a consequence of the scapular dorsal reorientation, and the demand for an extreme positioning of the elbow during arm-swinging (Larson, 1988). In the case of modern humans, they do not frequently use their forelimbs for climbing, so the lateral expansion of the subscapularis fossa is relatively small in relation to their body size (Larson, 1995).

Teres Minor

The teres minor is a muscle that is absent in phylogenetically plesiomorphic mammals, being derived from the deltoid complex (Inman *et al*, 1944; De Palma, 2008). When the infraspinous fossa started to progressively increase, a part of the deltoid separated from it, and started to increase too. Over the time, the skeletal changes have altered the position of this "new" muscle, permitting it to act upon the humerus in a downward direction (Inman *et al*, 1944; De Palma, 2008). According to Ashton and Oxnard (1963), in hominoids the teres minor is completely differentiated from the infraspinatus and deltoid muscles to form a separate unit. For a long time the teres minor was thought to form a functional group with the subscapularis and the infraspinatus (see above), depressing the head of the humerus and rotating it (Inman *et al*, 1944; Tuttle and Basmajian, 1978a, 1978b). However, we currently know that in general terms the teres minor is primarily a lateral rotator of the humerus, participating in the maintenance of the humeral head in position (Larson and Stern, 1986; Aiello and Dean, 1990; Jenkins, 2009).

It is important to highlight that the teres minor and, as we have seen above, a great part of the subscapularis, are not involved in the swing phase of the arm-raising (Larson and Stern, 1986), being only active during its support phase. This may indicate that, at least in arm-raising behaviors, teres minor helps in resisting transarticular tensile stresses at the glenohumeral joint (Larson and Stern, 1986), and as a retractor of the humerus during hoisting in orangutans (Tuttle and Basmajian, 1987a). That is, it is an adductor of the arm (Larson and Stern, 1986). During knuckle-walking, teres minor acts, at least in chimpanzee, in the rotation of the arm laterally (Larson and Stern, 1987). From this review we can conclude that of the muscles of the rotator cuff, the teres minor is the least studied and further studies are needed to better understand its function and evolution.

Conclusion

Understanding primate and human rotator cuff anatomy is crucial for enhancing our understanding of primate upper limb adaptations and thus of primate and human evolutionary history. Each muscle of the rotator cuff has its own role in the movement of the upper extremity, this role varying in different locomotor groups and being adapted to the functional requirements of each type of locomotion. Thus, if we understand how the rotator cuff muscles work in each locomotor groups, we can improve our understanding about which were the evolutionary processes that took place in the origin and evolution of the hominoids and thus of our lineage.

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2. A comparison of qualitative and quantitative methodological approaches to characterizing the dorsal side of the scapula in Hominoidea and its relationship to locomotion.

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RESUMEN

A pesar de los numerosos estudios realizados sobre la forma de la escápula de los primates, todavía no hay un acuerdo acerca de si existe una relación directa entre la morfología de la escápula y los comportamientos locomotores de los primates (Schultz 1930; Roberts 1974; Shea 1986; Inouye & Shea 1997; Taylor 1997; Ward 1997; Inouye & Taylor 2000; Taylor & Slice 2005; Young 2006, 2008). En este estudio se analiza mediante diferentes metodologías cualitativas y cuantitativas la relación entre la morfología de la cara dorsal de la escápula, especialmente la proporción entre las fosas supraespinosa e infraespinosa (S/I), y los comportamientos locomotores de los primates hominoideos, incluyendo humanos modernos.

El análisis de la morfometría geométrica 2D de la cara dorsal de la escápula, con el fin de comparar grupos locomotores, mostró diferencias significativas en la proporción S/I y en la longitud relativa y angulación de la espina de la escápula. También se observaron diferencias entre grupos en las proporciones entre las fosas supraespinosa e infraespinosa (S/I) medidas con diferentes índices: SFI (*spinal fossae index*, con medidas lineales), 2DI (áreas de las fosas en 2D) y 3DI (áreas de las fosas en 3D). Las diferencias morfológicas encontradas, tanto en el análisis cualitativo como en el cuantitativo, son un reflejo de los requerimientos funcionales asociados a cada tipo de locomoción. Los taxones *Homo* y *Pongo* comparten una morfología que se caracteriza por una fosa supraespinosa relativamente pequeña, relacionada con la necesidad de movimiento rápidos y precisión manipulativa en *Homo*, y con las adaptaciones a la vida arbórea en *Pongo*. Por el contrario, *Pan*, *Gorilla* e *Hylobates*

se caracterizan por una fosa supraespinosa relativamente grande, relacionada con la locomoción terrestre de los *knuckle-walkers* (*Gorilla* y *Pan*), y con la braquiación en *Hylobates*.

Finalmente, la comparación de estos índices de forma con la proporción entre los pesos de los músculos supraespinoso e infraespinoso, mostró que la proporción 3DI es la más fiable como estimador del índice de peso muscular (MWI) en ausencia de músculo. Los resultados obtenidos indican que no es posible hacer inferencias locomotoras exclusivamente a partir de medidas osteológicas ya que no existe una relación directa entre el tamaño de la inserción y del músculo. Los factores que pueden alterar esta relación son muy diversos (Zumwalt 2006).

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A Comparison of Qualitative and Quantitative Methodological Approaches to Characterizing the Dorsal Side of the Scapula in Hominoidea and Its Relationship to Locomotion

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Abstract Hominoidea have adapted to various forms of locomotion, each of which has specific requirements that are reflected in the shape of the scapula. We compared several qualitative and quantitative methods for characterizing the dorsal side of the scapula to detect morphological differences that reflect the adaptations of the scapula to locomotor behaviors. Our sample included 55 specimens of Hominoidea, representing five genera, including *Homo*, focusing specifically on the relative sizes of the scapular supraspinous and infranspinous fossae. In addition, we weighed the supraspinatus and infraspinatus muscles of 23 of the specimens to examine the feasibility of extrapolating muscle characteristics from osteological data. Our findings confirmed that the five genera exhibit significant differences in the relative size of the supraspinous and the infraspinous fossae that are related to their forms of locomotion. The supraspinous fossa was relatively small in *Homo* and *Pongo* but large in *Pan*, *Gorilla*, and *Hylobates*. The analysis of muscle weights showed that a substantial amount of information about soft tissues is lost in osteological analyses, leading us to recommend caution when drawing conclusions regarding forms of locomotion based only on osteological analyses.

Keywords 2D geometric morphometrics · 3D areas · Hominoidea · Infraspinatus · Scapula · Supraspinatus

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Introduction

Extant hominoids (*Homo*, *Pan*, *Gorilla*, *Pongo*, and *Hylobates*) share an orthograde locomotion body plan (Aiello and Dean 1990; Gebo 2010; Larson 1993) characterized by a vertical, transversely broad, and dorsoventrally shallow thorax and a laterally oriented glenoid fossa of the scapula. This lateral orientation increases the mobility of the glenohumeral joint greatly, allowing free overhead elevation of the arm in the scapular plane (Larson 1993; Roberts 1974) and a great variety of locomotor behavior patterns. Within the extant apes, hylobatids are the most arboreal, performing true brachiation, suspending and propelling the body below tree branches without using the lower limbs (Fleagle 1999; Napier 1963; Tuttle 1975). Orangutans (*Pongo*) rarely move on the ground, traveling cautiously through the upper levels of the canopy using quadrumanous climbing and arm-hanging (Fleagle 1999; Thorpe and Crompton 2005, 2006; Ward 2007). Chimpanzees (*Pan*) are mostly arboreal when they forage, hunt, and sleep, but they spend much of their time as terrestrial knuckle-walkers (Fleagle 1999; Goodall 1965). Gorillas (*Gorilla*), the largest living primates, are almost exclusively terrestrial, although they sporadically climb trees, especially for feeding and sleeping (Doran 1996; Fleagle 1999; Kuroda 1992; Tutin and Fernandez 1985; Tuttle and Watts 1985; Remis 1995). Modern humans, with obligate bipedal locomotion, have an upper limb that is almost exclusively a manipulative extremity (Fleagle 1999; Oxnard 1969; Ziegler 1964). Despite some overlap in locomotor repertoires among the hominoids, we can observe the specificities of their locomotor behaviors in the morphology of their scapular bone.

The scapula is the forelimb bone that varies most in shape among primates (Oxnard 1967) because its morphology depends largely on muscular function during locomotion (Ashton and Oxnard 1963; Inman *et al*. 1944; Larson 1993, 1995; Larson and Stern 1986, 1987, 1989, 1992; Larson *et al*. 1991; Oxnard 1967, 1968, 1969; Oxnard and Neely 1969; Roberts 1974; Shea 1986). The scapulae of quadruped mammals, which are affected mainly by compressive forces, are long (reaching from the vertebral border to the glenoid fossa) and narrow (from the superior to the inferior angles), whereas the scapulae of suspensory primates, affected mainly by tensile forces during locomotion, are shorter and wider (Ashton and Oxnard 1963, 1964; Ashton *et al*. 1965; Larson 1993; Schultz 1930). However, this morphological dichotomy ignores intermediate shapes of scapular bones because the variation in the osteological and muscular anatomy of the shoulder actually forms a fairly continuous spectrum, as observed in spider monkeys of the genus *Ateles* (Larson 1993; Oxnard 1967).

The shape of the scapula is determined largely by the rotator cuff muscles (subscapularis, supraspinatus, infraspinatus, and teres minor), which attach to its fossae. The spine, the acromion, and the margins of the scapula also serve as attachments of muscles of the upper limb, back, and neck. These muscles, including the deltoid, trapezius, levator scapulae, rhomboid major and minor, serratus anterior, latissimus dorsi, and teres major all also influence, to some extent, the shape of the scapula. The rotator cuff muscles play an important role in the movement and stabilization of the glenohumeral joint in primates (Ashton and Oxnard 1963; Potau *et al*. 2009; Roberts 1974; Wolffson 1950). Inman *et al*. (1944), in a classic electromyographic study of the human arm during elevation, described a force couple operating in concert at the glenohumeral joint, the deltoid and supraspinatus muscles providing the power for arm elevation, with the infraspinatus, teres minor and subscapularis compensating the superior displacement of the humerus. Tuttle and Basmajian (1978a,b) concluded that this force couple model existed not only in humans but also in all the great apes. However, this force couple model has since been shown to be imprecise, because all the rotator cuff muscles have been shown to be essential for the active stabilization of the glenohumeral joint (Larson and Stern 1986, 1987; Roberts 1974), each having a specific role during arm movements (Larson and Stern 1986, 1987); see Bello-Hellegouarch *et al*. (2012) for further information about the rotator cuff muscles. The subscapularis is mainly a medial rotator and adductor of the arm (Larson 1988; Larson and Stern 1986). The supraspinatus is an abductor muscle that assists the deltoid in providing strength during the abduction of the upper limb in free arm movements (Inman *et al*. 1944; Larson and Stern 1986; Tuttle and Basmajian 1978a), also bearing the main responsibility for preventing the superior displacement of the humeral head caused by the deltoid and for stabilizing the humerus during the initial phase of brachial elevation (Howell *et al*. 1986; Larson and Stern 1986; Thompson *et al*. 1996). It is also essential to resist humeral displacement, stabilizing the glenohumeral joint during the support phase of quadrupedal postures, such as during knuckle-walking (Larson and Stern 1987, 1989, 1992). The infraspinatus is a lateral rotator of the humerus that acts as the primary synergist to the deltoid in motions combining lateral rotation with arm abduction, such as overhead reaches and vertical climbing (Larson and Stern 1986). In addition, the infraspinatus is the principal muscle that stabilizes the glenohumeral joint during pendant suspension and the support phase of arm-swinging (Larson and Stern 1986; Roberts 1974) and, together with the supraspinatus, during the support phase of knuckle-walking (Larson and Stern 1987; Tuttle and Basmajian 1978b). The teres minor is a lateral rotator (Inman *et al*. 1944; Larson and Stern 1986), and on some occasions, e.g., during hoisting in the orangutan, it can act as adductor of the arm (Tuttle and Basmajian 1978a, b).

The ratio between the sizes of the supraspinous and infraspinous fossae is one of the most used parameters relating the morphology of the scapula with the functional anatomy of the rotator cuff muscles. Classical studies (Frey 1923; Inman *et al*. 1944; Roberts 1974; Schultz 1930) used the spinal fossae index (SFI), the supraspinous/infraspinous fossae breadth ratio, to compare the morphology of the dorsal side of the scapula among different primate species and make inferences regarding their differential anatomies and forms of locomotion. Some of the results obtained with this index indicated that the infraspinous fossa is larger than the supraspinous one in arboreal primates, and both fossae are larger than in terrestrial primates (Roberts 1974). The supraspinous fossa of knuckle-walkers —and especially of gorillas— is the largest relative to the infraspinous fossa, perhaps due to the hypertrophy of the supraspinatus caused by the dorsal position of the scapula in knuckle-walkers, which places additional demands on the supraspinatus to resist shearing stresses at the glenohumeral joint (Roberts 1974). Orangutans, however, have the largest infraspinous fossa relative to the supraspinous fossa, reflecting their quadrumanous climbing and suspensory habits (Roberts 1974; Schultz 1930). Humans have a relatively small supraspinous fossa, a reflection of their use of the arm with the humerus held below the shoulder (Roberts 1974).

More recent studies of scapular shape have used landmark-based geometric morphometrics (GM), an analysis of geometric information based on a configuration of landmarks independent of size, position, and orientation (Dryden and Mardia 1998) providing informative and intuitive graphic displays of shape changes. GM has been used to study scapular shape variation in several groups of vertebrates, including squirrels (Swiderski 1993), armadillos (Monteiro and Abe 1999), turtles (Depecker *et al*. 2006), rodents (Morgan 2009), and marsupials (Astúa 2009), as well as primates, although in this case the findings were inconsistent. Taylor and Slice (2005) used two-dimensional GM to compare the shape of the dorsal side of the scapula, including the fossae, the spine, and the acromion, of chimpanzees with that of gorillas. They found differences in scapular shape between chimpanzees and gorillas, as well as between the two gorilla species they analyzed (*Gorilla beringei* and *G. gorilla*), but found no functional pattern of differentiation across taxa. This lack of a clear link between scapular shape and locomotion was consistent with previous conventional studies of African ape scapular morphology (Inouye and Shea 1997; Inouye and Taylor 2000; Shea 1986; Taylor 1997), suggesting that differences in scapular shape among hominoids might be too subtle to reflect differences in locomotor behavior accurately (Ward 1997). Nevertheless, Young (2008), employing three-dimensional GM to compare ontogenetic shape variation in the scapula of different anthropoids, found that the main factor influencing scapular shape was function, as there was a substantial convergence in shape driven by functional similarities, with some evidence of phylogenetic influence during infancy. Moreover, this pattern of shape did not seem to change during ontogeny, being determined prenatally and remaining constant after birth (Young 2006). Although Young (2006, 2008) analyzed intra- and interspecific shape variation in his GM studies, he neither quantified it nor included humans in the numerous species of primates he studied.

Despite the numerous studies of scapular shape, some authors consider that we still lack an overall consensus on the interdependence between the scapular fossae ratio and locomotor behaviors in the Hominoidea (Inouye and Shea 1997; Inouye and Taylor 2000; Shea 1986; Taylor 1997; Taylor and Slice 2005; Ward 1997), whereas others suggest a clear association between scapular shape and locomotion (Roberts 1974; Schultz 1930; Young 2006, 2008). In this study we attempt to clarify the relationship between the supraspinous/infraspinous fossae ratio and locomotor behaviors in hominoids, including *Homo*, by comparing the results obtained with different methods applied to the same scapulae sample. First, we conducted a two-dimensional geometric morphometric analysis of the dorsal side of the scapula to obtain qualitative information on scapular shape differences among hominoid groups. Next we analyzed scapular shape morphology focusing on supraspinous/infraspinous ratios using scapular linear dimensions, as in the classic spinal fossae index, and 2D and 3D measures of muscle insertion areas. We used the intergroup variability of these supraspinous to infraspinous fossae indices to make inferences about the evolution of locomotor behavior in hominoids. We predicted that the supraspinous/infraspinous ratio for the three-dimensional fossae areas would be the most informative measure of scapular function because it was an actual measure of muscle insertion areas and, thus, assumed to be informative concerning function. We calculated the index of supraspinatus to infraspinatus and teres minor muscles weights (the three muscles of the rotator cuff related to the supraspinous and infraspinous fossae) to test whether the information derived from the osteological analyses was consistent with the soft-tissue data. We obtained muscle weight information from dissections for some of the hominoid specimens studied because they were previously used in myosin expression analyses of the rotator cuff muscles that required cryopreservation of muscle tissues (Potau *et al.* 2011). This preservation procedure makes macroscopic information on muscular bellies or fibers hard to observe. However, because muscle weight correlates with its physiological cross-sectional area (PCSA), it may be a good indicator of the force capacities of muscles (Kikuchi 2010), allowing direct comparisons with the scapular shape analysis.

Materials and Methods

We obtained the scapulae of 55 Hominoidea primate specimens (Table I) from four institutions: the Museum of Natural Sciences, Barcelona, Spain ($N=14$); the Anatomical Museum of the University of Valladolid, Spain ($N=20$); the Royal Institute of Natural Sciences in Brussels, Belgium ($N=9$); and the Unit of Human Anatomy and Embryology of the University of Barcelona, Spain ($N=12$). All the nonhuman specimens studied were adult captive individuals of unknown age at death, and the human samples consisted of adult specimens with known ages at death. The specimens were representative of the five main locomotor behaviors according to Schmitt (2010), whose locomotor classification we adopted because of its simplification of the diverse locomotor behavior patterns performed by the hominoids.

Table I Number of specimens analyzed, samples dissected (in parentheses), and form of locomotion (according to Schmitt 2010) for each of the hominoid species included in the study

Species	Male	Female	Unknown	Total	Form of locomotion
Hylobates gabriellae	1 (1)			1 (1)	Arboreal brachiator
Hylobates lar	1	7		8	Arboreal brachiator
Hylobates syndactylus	1		1	2	Arboreal brachiator
Hylobates klossi	1			1	Arboreal brachiator
Pan paniscus	1			1	Arboreal arm-swinger/terrestrial knuckle-walker
Pan troglodytes	5 (3)	7 (1)		12 (4)	Arboreal arm-swinger/terrestrial knuckle-walker
Pongo pygmaeus	1	6 (3)		7 (3)	Arboreal arm-swinger/arboreal quadrumanous
Gorilla gorilla	5 (1)	6 (2)		11 (3)	Terrestrial knuckle-walker
Homo sapiens	6 (6)	6 (6)		12 (12)	Biped
Total	20 (11)	34 (12)	1	55 (23)	

GM Analysis

Following Bookstein's nomenclature (1991), we defined nine anatomical landmarks for the GM analysis (Table II; Fig. 1). Seven of them (all except landmarks 5 and 8) have been considered operationally homologous and representative of scapular shape (Ashton and Oxnard 1964; Ashton *et al.* 1976; Larson 1993, 1995; Oxnard 1967; Roberts 1974; Schultz 1930; Shea 1986; Taylor 1997; Taylor and Slice 2005; Young 2006, 2008). Landmarks 5 and 8 are indicative of the origin of the teres major muscle, differentiating the infraspinatus and teres minor insertion areas from that of the teres. We considered the infraspinatus and teres minor muscles together because both act mainly as lateral rotators of the glenohumeral joint (Larson and Stern 1986, 1987; Tuttle and Basmajian 1978a, b).

We defined all the landmarks on 2D digital images of the scapular blades. Because scapulae are not perfectly flat, some dimensions may be distorted when we represent 3D objects in two dimensions. To minimize this, we kept the distance to the digital camera constant and oriented the scapulae with the plane defined by landmarks 3, 4, and 5 parallel to the plane of focus. The distortion caused by projecting all landmarks onto this plane will have its greatest effect on the acromion (Swiderski 1993), not affecting our analysis. After obtaining the digital images with a Canon EOS 550D digital camera we recorded the coordinates of the landmarks with tpsDig 2.16 software. We used MorphoJ 1.02 to conduct the GM analyses, which provides an integrated and easy environment for standard multivariate analyses used in phylogenetic applications, quantitative genetics, and analyses of modularity in shape data (Klingenberg 2010). GM analyses are based on a General Procrustes analysis, a procedure that removes variability due to size, position, and orientation (Bookstein 1991; Dryden and Mardia 1998; Klingenberg 2010; Zelditch *et al.* 2004) and minimizes the sum of square distances between equivalent landmarks (O'Higgins 2010; Rohlf and Slice 1990). The resulting data set, known as Procrustes residuals, can then be used for multivariate statistical analyses (Bookstein 1991; Dryden and Mardia 1998; Klingenberg 2010; Rohlf and Marcus 1993; Zelditch *et al.* 2004).

Table II Type and description of landmarks used in the GM analysis

Landmark	Type[a]	Name/definition
1	II	Suprascapular notch
2	III	Superior angle of the scapula
3	I	Intersection between vertebral border and base of scapular spine
4	II	Spinoglenoid notch
5	I	Intersection point of the teres major fossa and the vertebral border of the scapula
6	III	Inferior angle of the scapula
7	III	Lateral expansion of the teres major fossa
8	I	Intersection point of the teres major fossa and the lateral border of the scapula
9	II	Infraglenoid tubercle

[a] Bookstein *et al.* 1991; O'Higgins 2010.

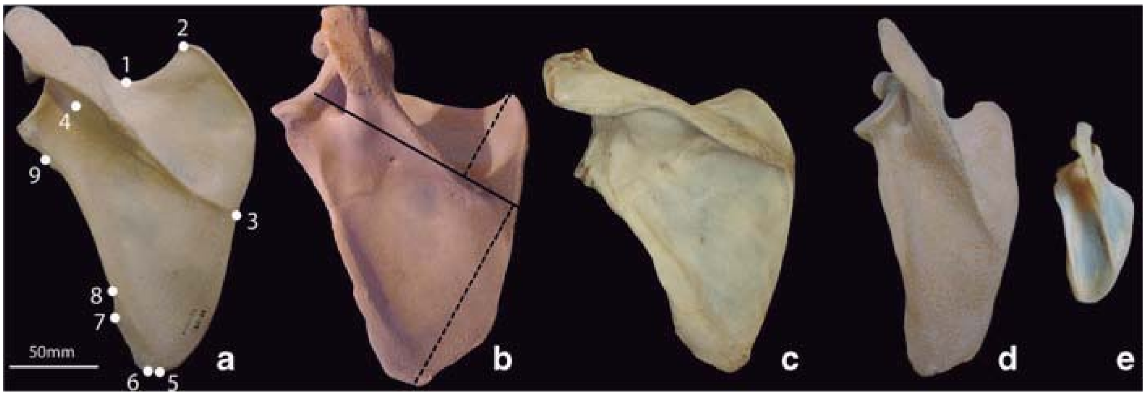

Fig. 1 Dorsal view of the scapulae of (**a**) *Gorilla*, (**b**) *Pongo*, (**c**) *Homo*, (**d**) *Pan*, and (**e**) *Hylobates*. Landmarks used in the GM analysis are shown for the scapula of *Gorilla*. Linear measurements used to obtain the SFI are shown for the scapula of *Pongo*. The orientation of the scapulae was made with all superior borders aligned.

We conducted a principal components analysis (PCA) to assess the main shape variations among samples (Klingenberg 2010). PCA incorporates and reduces complex multidimensional data to a few simple variables known as eigenvectors (Klingenberg 2010; O'Higgins 2010; Zelditch *et al*. 2004). We then performed a multivariate regression analysis of shape to rule out allometric scaling (Bookstein 1991; Gould 1966), the potential influence of size on variation in shape, by describing the percentage of variance predicted to be related to size (Klingenberg 2010; O'Higgins 2010; Zelditch *et al*. 2004). The main principal component, indicative of shape, was the dependent variable, and the logarithm of the centroid size, indicative of size, was the independent variable (Klingenberg 1996; O'Higgins 2010). With MorphoJ it is possible to perform multivariate regressions with a permutation test with 1000 randomizations and to pool the regression within given subgroups (genus in this case) as an external variable, making it ideal when a correction of size among groups is required.

We analyzed differences in scapular shape between groups using canonical variates analysis (CVA). CVA finds the maximum variation among *a priori* groups, in our case type of locomotion. The canonical variates derived from the analysis maximize the shape differences between groups (Klingenberg 2010; Zelditch *et al.* 2004), which can be represented as landmark displacements with regard to the mean shape along the canonical variate. We tested the reliability of group differences found in the CVA using linear discriminant analysis (LDA), with Fisher's classification rule and a leave-one-out, jackknife cross-validation method to obtain the *post hoc* probabilities of correct classification (Klingenberg 2010). Finally, we used the Mahalanobis distances derived from the CVA to plot an unweighted pair group method with arithmetic mean (UPGMA) unrooted tree, using the PHYLIP 3.5C NEIGHBOR package, which shows shape similarities among groups in a hierarchical phenetic tree assuming constant rates of evolution.

Quantitative Analyses

Using AnalySYS, we calculated the SFI (Frey 1923) by measuring the supraspinous and infraspinous fossae breadths (in mm) perpendicular to the line defined by the distance from the midpoint on the dorsal border of the glenoid fossa to the intersection between the scapular spine and the vertebral border (Frey 1923; Schultz 1930) (Fig. 1). We then calculated the two-dimensional index (2DI) by measuring two-dimensional areas (in mm^2) of the supraspinous and infraspinous fossae, using the digital images obtained for the GM analysis. We defined the perimeters of the fossae with SigmaScan (SPSS™) to obtain the two-dimensional areas required for computation of the supraspinous/infraspinous ratio. Finally, we calculated the three-dimensional index (3DI) by measuring the three-dimensional areas (in mm^2) of the scapular insertion surfaces of the supraspinatus, infraspinatus, and teres minor muscles, using a Picza LPX-600 3D laser scanner (Roland DGA Co.). Because laser reflectance on original bones was poor, we scanned high-quality molds of the fossae made with polysiloxane condensation-type silicone elastomer (Coltène Speedex Putty, Coltène/Whaledent AG). Scan dot resolution was 0.4 mm. We saved the three-dimensional coordinates of scanned points in Drawing Exchange Format (.dxf) and measured the areas of the insertions with Rhinoceros 3.0 after cutting the three-dimensional mesh at the insertion area border.

We used the Kolmogorov–Smirnov test to check the normal distribution of the data and the ANOVA tests and Bonferroni *post hoc* comparisons to test for differences in locomotor group means. We also tested how reliably the three quantitative indices discriminated locomotor groups using LDA, followed by a *post hoc* correct classification analysis with leave-one-out, jackknife cross-validation. We plotted a UPGMA tree based on the squared Euclidean distances of the three quantitative analyses, and compared it with the tree obtained in the GM analysis by using a Mantel test (XLSTAT™) with 1000 permutations to determine the correlation between the distance matrices of both trees.

Muscle Weight Index

We measured the weights of the rotator cuff muscle in 12 human and 11 nonhuman shoulders that had been cryopreserved 24–48 h after death and not treated with any fixation method. The same researcher (J. M. Potau) dissected all the muscles and recorded the origin and insertion of each rotator cuff muscle. He then removed each muscle, cleaned it of adipose tissue and muscle fascia, and weighed it. We calculated the ratios of the supraspinatus to infraspinatus + teres minor weights. The 12 human cadavers (six males and six females), showing no signs of macroscopic pathological conditions, came from the Body Donation Service and dissection rooms of the University of Barcelona. Ages at death ranged from 38 to 80 yr (mean 65 yr; mode 60 yr). The 11 nonhuman primates (one *Hylobates gabriellae*, three *Pongo pygmaeus*, three *Gorilla gorilla*, and four *Pan troglodytes*) were provided by the Department of Anatomy and Radiology of the University of Valladolid, Spain. They had lived in captivity in various Spanish zoos and their deaths were unrelated to our study. One *Pongo* and one *Pan* were provided at the last minute and could be included in the quantitative analysis of the supraspinous and infraspinous fossae but not in the GM analysis. We compared the muscle weight indices with the three quantitative indices (SFI, 2DI, 3DI) obtained in the 23 samples. However, owing to the relatively small samples available for some specimens in this comparison, we were cautious in drawing definite conclusions that need to be confirmed with a larger sample.

Results

GM Analysis

The first two principal components (PC1 and PC2) of the PCA derived from the Procrustes residuals explained 70.27 % of scapular shape variation (56.88 % PC1, 13.38 % PC2). The specimens clearly clustered by type of locomotion in the plot of PC1 vs. PC2 (Fig. 2). Both the bipedal *Homo* and the arboreal quadrumanous and arm-swinger *Pongo* showed minimum values for PC1, though they differed for PC2, whereas the arboreal brachiator *Hylobates* showed the highest values for PC1. Although *Pan* and *Gorilla* showed intermediate values for PC1, the arboreal arm-swinger and terrestrial knuckle-walker *Pan* had slightly higher PC1 values than the mostly terrestrial knuckle-walker *Gorilla*. *Pan* and *Gorilla* showed the highest mean values for PC2. The multivariate regression analysis (with 1000 permutations) of PC1 and PC2 and the logarithm of the centroid size (logCS) indicated that neither PC1 ($P=0.20$), with 5.63 % of total shape variation explained by size variation, nor PC2 ($P=0.22$), with 0.96 % of total shape variation explained by size variation, correlated significantly with logCS, indicating that size allometry had little effect on scapular shape variation.

Three canonical variates (CV1, CV2, and CV3) (Fig. 3) derived from the CVA explained 93.43 % of scapular shape variation. In the LDA, using Mahalanobis distances to calculate differences between mean scapular shapes, all pairwise group comparisons were significant (Table III) except that between *Pongo* and *Hylobates*, which was significant when the Procrustes permutation test was used (Table III). The *post hoc* correct classification probabilities derived from the LDA after leave-one-out jackknife cross-validation varied 66.7–100 % depending on sample size (Table IV). CV1 explained 62.75 % of total variance and was indicative of the increase in the angulation of the scapular spine (displacement of landmark 3 toward landmark 5; Fig. 3) that results in the increase in size of the supraspinous fossa in relation to the

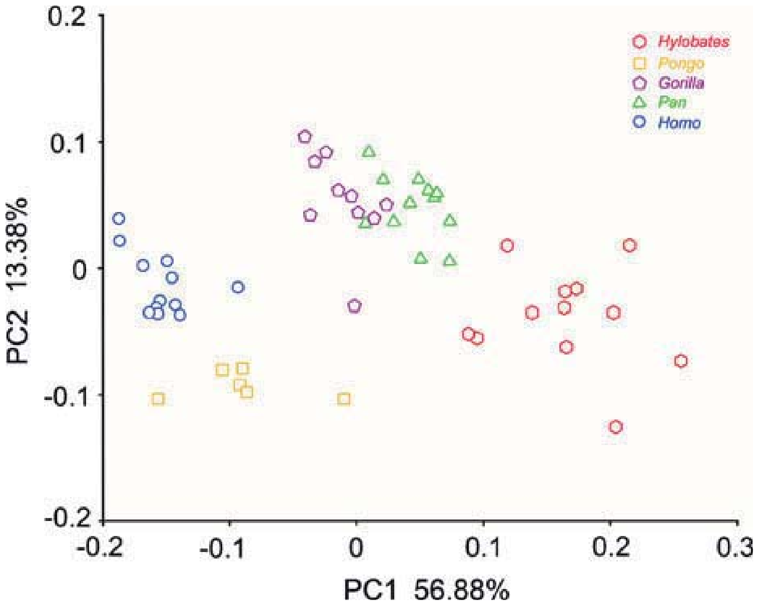

Fig. 2 Scatterplot of the first two principal components (PC1 and PC2) derived from the PCA of the GM analysis.

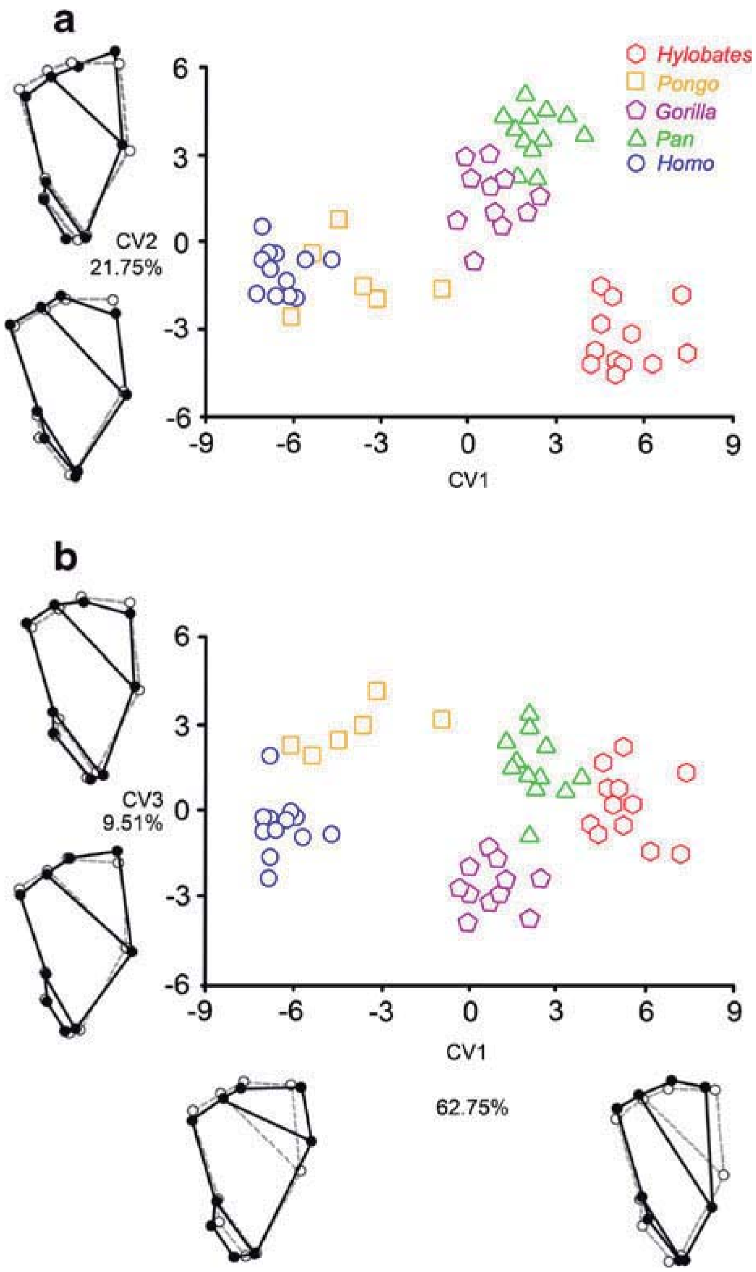

Fig. 3 Scatterplots showing the dispersion of the locomotor groups for (**a**) CV1 vs. CV2 and (**b**) CV1 vs. CV3. Solid black wireframes shots show the extreme shape of each CV and the dashed gray wireframes shots represent the mean shape (coordinates 0, 0).

infraspinous fossa, the elongation of the scapular spine, and the reduction of the teres major insertion area (landmarks 6 and 7 becoming closer). *Homo* and *Pongo*, the only groups with negative CV1 values, have short scapular spines, oriented perpendicularly to the vertebral border, relatively small supraspinous fossae compared to the infraspinous fossae, and large teres major insertion areas. In contrast, *Hylobates*, with the highest positive CV1 values, have a long, more angulated spine; similar supraspinous and infraspinous fossae sizes; and a small teres major insertion area. *Pan* and *Gorilla* had intermediate CV1 values between these two extremes. CV2 explained 21.75 % of total variance and was indicative of a reduction of scapular length (inward displacement of landmarks 3 and 4; Fig. 3), maintenance of the spinal angle, and an increase of the sharpness of the superior angle of the scapula (outward displacement of landmark 2). *Hylobates*, with the lowest CV2 values, had a long scapular blade and

Table III Mahalanobis and Procrustes (in italics) distances between groups with *P*-values (in parentheses) based on 1000 permutations

Species	Mahalanobis distance (*P* value) *Procrustes distance* (*P value*) *Gorilla*	*Homo*	*Pan*	*Pongo*
Homo	18.43 (<0.0001)			
	0.18 (<0.0001)			
Pan	7.44 (0.0023)	17.82 (0.0001)		
	0.11 (<0.0001)	*0.22 (<0.0001)*		
Pongo	37.33 (0.0192)	20.22 (0.0135)	14.48 (0.0351)	
	0.18 (<0.0001)	*0.13 (<0.0001)*	*0.20(<0.0001)*	
Hylobates	12.75 (<0.0001)	25.48 (<0.0001)	13.74 (<0.0001)	11.92 (0.0601)
	0.21 (<0.0001)	*0.32 (<0.0001)*	*0.17 (<0.0001)*	*0.27 (<0.0001)*

a less sharp superior angle, whereas *Pan*, with the highest CV2 values, showed a short scapular blade and a sharper superior angle. *Homo* and *Pongo* had intermediate CV2 values and *Gorilla* were midway between *Pongo* and *Pan*. CV3 explained only 9.51 % of total variance. It was indicative of a decrease in the sharpness of the superior angle (downward displacement of landmark 2) and an increase in the length of the teres major insertion area (outward displacement of landmarks 5 and 6; Fig. 3).

Quantitative Analyses

The means and standard deviations of SFI, 2DI, and 3DI for each locomotor group are shown in Table V, all variables following normal distributions within locomotor groups. *Homo* had the lowest values in all three indices, followed by *Pongo* and *Pan*. *Gorilla* had the highest 2DI value, while *Hylobates* had the highest SFI and 3DI values. We found significant differences among locomotor groups in all three indices (ANOVA: 2DI $F=42.13$, $P<0.001$, 3DI $F=21.96$, $P<0.001$, SFI $F=17.78$, $P<0.001$). Bonferroni *post hoc* comparisons showed significant differences for all

Table IV Percentages of *post hoc* correct classification probabilities derived from the discriminant functions after leave-one out cross-validations for the canonical variate shape analysis (CVA) and the discriminant quantitative analysis (DA)

	CVA	DA
Pongo–Hylobates	66.7	100
Pongo–Pan	77.8	79.2
Pongo–Homo	88.9	58.4
Pongo–Gorilla	88.2	100
Hylobates–Pan	100	75.0
Hylobates–Homo	100	100
Hylobates–Gorilla	91.3	83.4
Pan–Homo	95.8	100
Pan–Gorilla	91.3	86.4
Homo–Gorilla	100	100

pair-group comparisons except *Homo–Pongo* and *Gorilla–Pan* for SFI; *Pongo–Homo* and *Hylobates–Gorilla* for 2DI; and *Homo–Pongo*, *Gorilla–Pan*, and *Gorilla–Hylobates* for 3DI (Table VI). The LDA based on these indices yielded three discriminant functions, the first two of which showed significant intergroup differences, explaining 99.7 % of total variance, with DF_1 correlating mainly with 2DI and DF_2 with SFI (Table VII). The 2DI and 3DI indices discriminated locomotor groups more efficiently than SFI (Fig. 4). *Gorilla* and *Hylobates* had higher 2DI and 3DI values (a larger supraspinous fossa in relation to the infraspinous fossa), whereas *Pongo* and *Homo* had lower 2DI and 3DI values (a smaller supraspinous fossa in relation to the infraspinous fossa) and *Pan* had intermediate values. Within the LDA, the lowest *post hoc* probability of correct classification (58.4 %) after the leave-one-out cross-validation was observed in the *Pongo–Homo* comparison (Table IV), most likely due to the misclassification of some *Pongo* specimens as *Homo*, as *Homo* showed a correct classification of 100 %.

In the 23 samples available, *Homo* had the lowest muscle weigh index (MWI), followed by *Pan*, *Pongo*, *Hylobates*, and *Gorilla*. The dispersion and variability of the MWI was most closely matched by the 3DI variable for all groups except *Homo* (Table VIII). This was as expected because the 3DI was obtained from actual measurements of 3D insertion areas, not from approximations, as was the case for SFI and 2DI.

In the UPGMA phenetic dendograms derived from the GM results and the quantitative indices (Table IX), *Homo* and *Pongo* closely resembled each other on one side, and *Pan* and *Gorilla* resembled each other on the other side, whereas *Hylobates* appeared as an outgroup to all other taxa, but closer to *Pan* and *Gorilla* (Fig. 5a). *Homo* and *Pongo* were farther from all other taxa in the dendogram derived from the quantitative indices (Fig. 5b) than in the GM dendogram. Nevertheless, the two distance matrices correlated significantly (Mantel test: r=0.813, P=0.005), indicating that the indices provided reliable information about shape variation.

Discussion

GM Analysis

The GM study showed that differences in the hominoid scapular shape are not related to allometric changes and may well be related to differences in locomotor behavior. This is in accordance with Davis (1964) and Müller (1967), who observed that the mammalian scapula as a whole was not subject to allometric changes, as differences in the scapular shape were independent of body size. Young (2008) also concluded that the major factor influencing scapular shape in primates was functional, although some evidence of phylogenetic influence was apparent in infants. Our GM analysis detected significant differences among locomotor groups, consistent with previous GM studies (Young 2008), with *Hylobates* having a distinct scapular shape and *Homo* and *Pongo* resembling each other and separated from *Gorilla* and *Pan*.

The main differences in scapular shape identified by the GM analysis were related to variation in the supraspinous:infraspinous fossae ratio and the angulation and relative length of the scapular spine. These two parameters are directly correlated

Table V Mean and standard deviation (in parentheses) of the SFI, 2DI, 3DI, and MWI indices by genera, representative of distinct locomotor groups

Genus	*N*	2DI	3DI	SFI	*N*	MWI
Homo	12	0.105 (0.025)	0.434 (0.076)	0.342 (0.035)	2	0.376 (0.074)
Pan	13	0.311 (0.050)	0.597 (0.111)	0.673 (0.085)	4	0.413 (0.050)
Pongo	7	0.177 (0.066)	0.466 (0.038)	0.374 (0.104)	3	0.458 (0.031)
Hylobates	12	0.448 (0.122)	0.696 (0.088)	1.007 (0.429)	1	0.591 (–)
Gorilla	11	0.510 (0.125)	0.676 (0.067)	0.714(0.098)	3	0.691 (0.102)

because, although other muscles that insert in the scapular spine have some influence on its orientation, e.g., the deltoid and the trapezius, the orientation of the scapular spine in suspensory primates is mainly related to the dorsal members of the rotator cuff and the role they play during arm-swinging and suspension (Larson and Stern 1986; Larson *et al*. 1991).

The knuckle-walkers *Gorilla* and *Pan* have a less angulated spine than *Hylobates* but more angulated than *Pongo* and *Homo*, having relatively large supraspinous fossae (Aiello and Dean 1990; Potau *et al*. 2007; Roberts 1974; Schultz 1930; Young 2008). This large supraspinous fossa may be related to the important role of the supraspinatus as a postural muscle during knuckle-walking, where it acts together with the infraspinatus to stabilize the glenohumeral joint by controlling the humeral retraction during the support phase (Larson and Stern 1987, 1992; Potau *et al*. 2009; Roberts 1974; Tuttle and Basmajian 1978b). The supraspinatus also acts to resist shearing stresses at the glenohumeral joint because of the dorsal position of the scapula in knuckle-walkers (Larson 1993; Roberts 1974). The differences we found between the two knuckle-walkers in our GM analysis may be explained by their locomotor differences. Chimpanzees are highly arboreal but spend much of their time as terrestrial knuckle-walkers (Fleagle 1999; Goodall 1965; Ward 2007), whereas gorillas are almost exclusively terrestrial, although they climb occasionally (Fleagle 1999; Remis 1995; Tuttle and Watts 1985; Ward 2007), particularly in the case of female western lowland gorillas (Doran 1996; Kuroda 1992; Tutin and Fernandez 1985). Although it has been suggested that much of the interspecific variation in morphology and behavior found between them chimpanzees and gorillas can be explained in terms of body size differences (Doran 1997; Isler 2005), some anatomical traits, especially those linked to specific behavioral differences, cannot (Doran 1997).

Homo is the hominoid with the least angulated spine and, therefore, with the greatest difference between the infraspinous and the supraspinous fossae. In modern humans, the habitual pendant position of the arm and the use of the upper limb almost exclusively as a manipulatory organ (Larson 1993, 1995; Potau *et al*. 2011) have decreased the shearing stresses at the glenohumeral joint, thus reducing the need for a developed muscle. Therefore, the human supraspinous fossa is relatively poorly developed (Potau *et al*. 2007; Roberts 1974). The reduced development of the supraspinatus muscle increases speed and precision during movements of the glenohumeral joint, essential in the manipulatory behaviors of the upper limb (Potau *et al*.

Table VI Results of Bonferroni *post hoc* tests comparing groups for the 2DI, 3DI, and SFI indices, showing the differences between the groups compared (d) and the significance of the comparisons (P)

	Pan ($N=13$)	*Pongo*	*Homo*	*Gorilla*
Pongo	2DI ($d=-0.134$, $P=0.019$)			
($N=7$)	3DI ($d=-0.131$, $P=0.016$)			
	SFI ($d=-0.299$, $P=0.044$)			
Homo	2DI ($d=-0.207$, $P<0.001$)	2DI ($d=-0.723$, $P=0.895$)		
($N=12$)	3DI ($d=-0.164$, $P<0.001$)	3DI ($d=-0.321$, $P=1.000$)		
	SFI ($d=-0.331$, $P=0.003$)	SFI ($d=-0.032$, $P=1.000$)		
Gorilla	2DI ($d=0.199$, $P<0.001$)	2DI ($d=0.333$, $P<0.001$)	2DI ($d=0.406$, $P<0.001$)	
($N=11$)	3DI ($d=0.788$, $P=0.258$)	3DI ($d=0.210$, $P<0.001$)	3DI ($d=0.242$, $P<0.001$)	
	SFI ($d=-0.041$, $P=1.000$)	SFI ($d=0.340$, $P=0.018$)	SFI ($d=0.372$, $P=0.001$)	
Hylobates	2DI ($d=0.137$, $P=0.003$)	2DI ($d=0.271$, $P<0.001$)	2DI ($d=0.343$, $P<0.001$)	2DI ($d=0.623$, $P=0.947$)
($N=12$)	3DI ($d=0.099$, $P=0.047$)	3DI ($d=0.231$, $P<0.001$)	3DI ($d=0.263$, $P<0.001$)	3DI ($d=-0.020$, $P=1.000$)
	SFI ($d=0.334$, $P=0.003$)	SFI ($d=0.633$, $P<0.001$)	SFI ($d=0.665$, $P<0.001$)	SFI ($d=0.293$, $P=0.019$)

Table VII Results of the LDA of the SFI, 2DI, and 3DI indices, showing the percent of total variance explained by each function, their correlation with the original variables, and the significance of the discrimination of the combined functions

DF	%	r_{2DI}	r_{3DI}	r_{SFI}
1	86.9	0.954	0.675	0.535
2	12.8	−0.050	0.347	0.812
3	0.3	−0.297	0.652	–0.233
CF	λ	df	*P*	
All	0.136	12	<0.001	
2–3	0.639	6	0.001	
3	0.989	2	0.757	

DF = discriminant function; % = percentage of total variance explained by each function; r_{2DI}, r_{3DI}, r_{SFI} = Pearson correlation coefficients between the discriminant functions and the indices; CF = contrasts of functions; λ = Wilks lambda statistic for the significance of the discrimination; df = degrees of freedom; *P* = significance value

2007), but reduces arm-raising ability compared to other hominoids (Ashton and Oxnard 1963, 1964; Larson 1993; Oxnard 1967, 1969). However, the infraspinatus muscle in modern humans is relatively large compared to the supraspinatus (Aiello and Dean 1990; Roberts 1974), owing to its need for external rotation during the elevation of the arm in the scapular plane, delaying the contact between the acromion and the greater tubercle of the humeral head (Basmajian and de Luca 1985; Inman *et al.* 1944).

Pongo, a highly arboreal and suspensory primate, is closer to *Homo* in the GM analysis than to the knuckle-walkers. A slightly angulated spine and a supraspinous

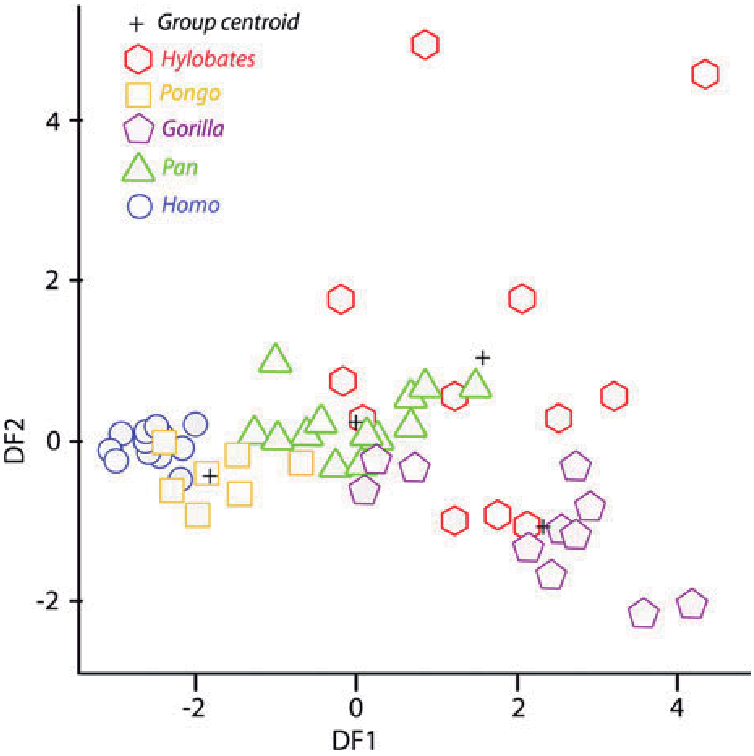

Fig. 4 LDA of the three quantitative indices (SFI, 2DI, and 3DI).

Table VIII Mean values and standard deviations (in parentheses) of the four indices considered by genera

Genus	*N*	MWI	2DI	3DI	SFI
Homo	12	0.38 (0.07)	0.11 (0.03)	0.43 (0.08)	0.34 (0.04)
Pan	4	0.41 (0.05)	0.29 (0.03)	0.53 (0.05)	0.62 (0.02)
Pongo	3	0.46 (0.03)	0.15 (0.07)	0.48 (0.04)	0.35 (0.05)
Hylobates	1	0.59 (-)	0.51 (-)	0.65 (-)	0.72 (-)
Gorilla	3	0.69 (0.10)	0.34 (0.02)	0.61 (0.04)	0.60 (0.04)

fossa that is poorly developed compared to the broad infraspinous fossa characterize *Pongo* (Oxnard 1984; Roberts 1974; Young 2008). The relatively well-developed infraspinatus confirms the important role of this muscle in suspensory behaviors. The external rotation function of the infraspinatus (assisted by the teres minor muscle) is especially important during the swing phase of vertical climbing and acts to resist transarticular tensile stresses during pendant suspension and during the support phase of arm-swinging (Larson and Stern 1986).

Hylobates has the most angulated spine, resulting in similar supraspinous and infraspinous fossae sizes. This hypertrophy of the supraspinous fossa cannot be explained by a postural function, as in knuckle-walkers, but may be due to the "overwhelming lineage-specific specializations" of their shoulder for true brachiation (Young 2008, p. 259). During the process of reaching upward when climbing vertically, *Hylobates* shows a degree of abduction of the humerus that is even larger than in the great apes, probably because of the smaller humeral head torsion in *Hylobates* (Isler 2002, 2005). Thus, the large supraspinous fossa found in *Hylobates* could be explained by the need of a great abductor for this purpose. Some studies have suggested that the shoulder abductors of the true brachiators are especially important for rapid accelerations of the forelimb, and in reaching for overhead supports that are not necessarily placed in the sagittal plane of the body (Michelsens *et al*. 2009, 2010). In addition, the infraspinatus muscle, as well as the rotators of the scapula, have a very important function stabilizing the body during brachiation, preventing it from swinging mediolaterally rather than forward (Kikuchi *et al*. 2012; Michelsen *et al*. 2009). The scapular shape difference between *Pongo* and *Hylobates* may seem surprising given the apparent suspensory behavior shared by both Asian apes. In contrast to the substantially larger orangutans, who owing to their large body size and weight adopt a slower and more cautious quadrumanous climbing

Table IX Mahalanobis distances derived from the CVA of the GM analysis and squared Euclidean distances (in parentheses) derived from the analysis of the indices, used to generate the UPGMA trees

	Gorilla	*Homo*	*Hylobates*	*Pan*
Homo	8.4015 (0.362)			
Hylobates	7.4750 (0.073)	12.1123 (0.629)		
Pan	5.3863 (0.109)	10.0748 (0.179)	7.8002 (0.152)	
Pongo	7.8738 (0.271)	5.9191 (0.007)	10.5180 (0.527)	8.8850 (0.130)

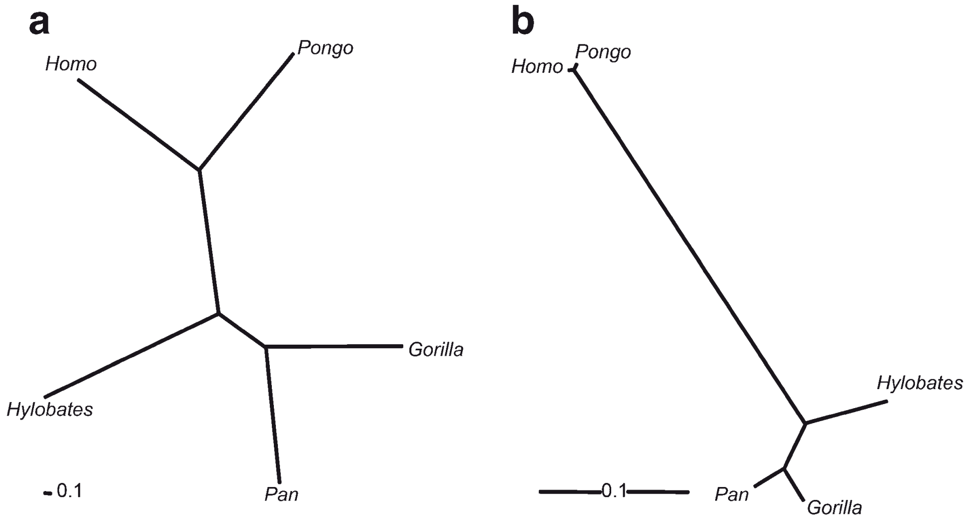

Fig. 5 UPGMA trees derived (**a**) from Mahalanobis distances between taxa according to the GM analysis and (**b**) from the squared Euclidean distances of the three quantitative indices.

and arm-hanging locomotion in the canopy (Fleagle 1999; Thorpe and Crompton 2005, 2006; Ward 2007), the smaller and lighter weighted gibbons propel their bodies quickly and effectively through the canopy using true brachiation, without the use of the lower limbs (Fleagle 1999; Napier 1963; Tuttle 1975).

Quantitative Analyses

The LDA identified *Pongo* and *Homo* as having low values for the three indices analyzed, indicating that they shared a smaller supraspinous in relation to the infraspinous fossa compared to *Gorilla*, *Pan*, and *Hylobates*. We found no significant differences between *Homo* and *Pongo* for any of the three indices, which is similar to the GM results, where *Homo* and *Pongo* slightly overlap. However, the results for *Pan*, *Hylobates*, and *Gorilla* are not so clear. We found significant differences between *Gorilla* and *Pan* in the 2DI, but none between *Gorilla* and *Hylobates*. There were no significant differences in the 3DI values between *Gorilla* and *Pan* or between *Gorilla* and *Hylobates*, either. Interestingly, the GM analysis found similarities between *Gorilla* and *Pan*, whereas the 2DI and the 3DI indices found similarities between *Gorilla* and *Hylobates*. In addition, although the 2DI and 3DI indices identified *Gorilla* and *Hylobates* as the two groups with the relatively larger supraspinous fossae, the GM analysis found that *Hylobates* had a slightly larger supraspinous fossa than *Gorilla*.

Homo always had the relatively smallest supraspinous fossa and the relatively smallest supraspinatus muscle. *Hylobates* always had the relatively largest supraspinous fossa but *Gorilla* had the largest supraspinatus muscle. We also found contradictory results for *Pan* and *Pongo*: Although in the dissected specimens the three quantitative indices showed that *Pongo* had a relatively smaller supraspinous fossa compared to *Pan*, the MWI showed that *Pongo* had a relatively larger supraspinatus muscle. These differences between the osteological and muscular data suggest that we must exercise caution when making inferences about muscle size and locomotor behavior based exclusively on the analysis of bones. For many years, researchers have reconstructed locomotor and postural behaviors of extinct species assuming that there was a direct and causative relationship between muscle size and bony attachments (Aiello and Dean 1990; Richmond and Strait 2000; Roberts 1974). However, a substantial part of the information about soft tissues is lost when we consider only osteological data because the size of the muscle may not be simply and directly reflected by the size of the fossa. Many factors besides muscle size or activity may influence this relationship in ways that are poorly understood (Zumwalt 2006), complicating the interpretation of the attachment morphologies. Thus, further work is needed to understand the influence of muscle size or its activity on bony attachments fully, particularly to make more reliable behavioral reconstructions from osteological data. The 3DI variable was the most similar to the muscular values, as one might expect. The 3DI values are true reflections of the area of attachment of the muscles because they include the curvature of the fossae and eliminate the parts of the blade that are not affected by the attachment of the rotator cuff muscles, e.g., teres major insertion area. Therefore, the 3DI appears to be the most accurate way to obtain functional information when the muscle is missing. However, our muscular sample size is limited, and further analyses with a larger sample are needed to confirm these preliminary conclusions.

Evolutionary Perspectives

The significant differences found in the ratios between the supraspinous and infraspinous fossae between the different locomotor groups lead us to speculate on the evolution of locomotor behavior in hominoids. The resemblance between *Pongo* and *Homo* suggests that the last common ancestor of the human–chimpanzee clade probably showed an overall suspensory shoulder girdle pattern (Crompton *et al.* 2008; 2010; Kivell and Schmitt 2009; McHenry 1986; Oxnard 1984; Thorpe *et al.* 2007), instead of a knuckle-walker structure, as has been suggested (Begun 1992; Corruccini and McHenry 2001; Orr 2005; Richmond and Strait 2000; Richmond *et al.* 2001; Williams 2010). In addition, despite the similarity found between *Gorilla* and *Pan*, they also showed somewhat distinct morphological patterns, supporting the independent evolution of knuckle-walking in the two taxa (Dainton and Macho 1999; Kivell and Schmitt 2009; Larson 1996), suggesting homoplasy between *Pan* and *Gorilla*. Finally, the fact that *Hylobates* separated completely from the other taxa supports the well-established hypothesis that *Hylobates* was the first hominoid to diverge (Groves 1972; Ruvolo 1997; Tuttle 1975; Young 2003), showing significant autapomorphies, such as a small body size along with highly derived brachiating specializations (Cartmill 1985) that differentiated them from other, more generalized hominoids.

Conclusions

We combined qualitative and quantitative methods to study the ratio between the supraspinous and infraspinous fossae of the scapula, confirming the presence of morphological differences that reflect the adaptations of the scapula to the main locomotor behavior of each group. *Homo* and *Pongo* share a distinct functional anatomy characterized by a relatively small supraspinous fossa related to the need for speed and manipulative precision in *Homo* and to adaptations to arboreality in *Pongo*. In contrast, *Pan*, *Gorilla*, and *Hylobates* are characterized by a relatively broad supraspinous fossa, related to the terrestrial locomotion of the knuckle-walkers *Pan* and *Gorilla* and to the highly specialized brachiation of *Hylobates*. An analysis of muscle weights revealed that, although a three-dimensional analysis of the fossae is useful when muscles are missing, substantial information about soft tissue is lost because the bony insertions do not necessarily reflect the size of the muscle. We must therefore be cautious when making locomotor inferences from osteological data alone. Further analyses with larger samples are required to confirm these preliminary conclusions.

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3. Brief communication: Morphological effects of captivity. A geometric morphometric analysis of the dorsal side of the scapula in captive-bred and wild-caught Hominidae.

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RESUMEN

Las colecciones osteológicas de primates procedentes de animales en cautividad son esenciales para estudiar las adaptaciones morfológicas del esqueleto a diferentes modos de locomoción, especialmente en especies en peligro de extinción. Sin embargo, se suelen descartar estas colecciones por no considerarse representativas de individuos en libertad ya que las condiciones de vida en cautividad podrían influir de manera crítica en la morfología del esqueleto (O'Regan 2001; O'Regan & Kitchener 2005). Factores ambientales, como la dieta, las características del sustrato o las restricciones climáticas, varían entre animales que viven en libertad y en cautividad, pero no se conoce con precisión si estas diferencias tienen un efecto significativo en la morfología del hueso (Zuccarelli 2004). A pesar de que algunos estudios han analizado esta influencia en la morfología craneal de algunos mamíferos (Hollister 1917; Groves 1982; O'Regan 2001; Zuccarelli 2004), ninguno se ha centrado en la influencia de las condiciones de cautividad en la morfología de la escápula de los primates. En este estudio se analiza la morfometría geométrica 2D de la cara dorsal de la escápula de varias especies de homínidos (*Gorilla gorilla*, *Pan troglodytes* y *Pongo pygmaeus*) procedentes tanto de cautividad como de libertad, con el fin de determinar si la vida en cautividad influye de un modo decisivo en la morfología de la escápula.

El análisis detectó las diferencias morfométricas entre especies, ya descritas en otros estudios anteriores (Young 2008; Bello-hellegouarch 2013a), pero en ningún caso se observaron diferencias significativas entre los especímenes procedentes de libertad y

de cautividad. Este resultado sugiere que la cautividad no afecta de manera significativa a la morfología de la escápula, al menos en la muestra analizada. Si esto se confirma en otras colecciones osteológicas, podríamos afirmar que los especímenes que han vivido en cautividad se pueden considerar representativos de la especie en su totalidad. Sin embargo, no es posible generalizar esta conclusión ya que diferentes huesos pueden responder de modos diferentes a los mismos estímulos externos (Fleagle & Meldrum 1988; Biewener & Gillis 1999; Pearson & Lieberman 2004; Plochocki *et al*. 2008; Green *et al*. 2012).

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Brief Communication: Morphological Effects of Captivity: A Geometric Morphometric Analysis of the Dorsal Side of the Scapula in Captive-Bred and Wild-Caught Hominoidea

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KEY WORDS 2D geometric morphometrics; scapula; captivity; Hominoidea

ABSTRACT Many osteological collections from museums and research institutions consist mainly of remains from captive-bred animals. The restrictions related to the space of their enclosures and the nature of its substrate are likely to affect the locomotor and postural behaviors of captive-bred animals, which are widely considered uninformative regarding bone morphology and anatomical adaptations of wild animals, especially so in the case of extant great apes. We made a landmark-based geometric morphometrics analysis of the dorsal side of the scapular bone of both wild-caught and captive-bred great apes to clarify the effect of captivity on the morphology of a bone greatly involved in locomotion. The comparison suggested that captivity did not have a significant effect on the landmark configuration used, neither on average scapular shape nor shape variability, being impossible to distinguish the scapulae of a captive-bred animal from that of a wild-caught one. This indicates that the analyzed scapulae from captive Hominoidea specimens may be used in morphological or taxonomic analyses since they show no atypical morphological traits caused by living conditions in captivity. Am J Phys Anthropol 152:306–310, 2013. © 2013 Wiley Periodicals, Inc.

Captive animals are essential for analyzing morphological adaptations in relation to locomotor behaviors in primate species since their osteological remains abound at numerous museum collections. This is especially the case for endangered species, for which a limited number of specimens are available and it is rarely feasible to measure extant specimens in their natural habitat. However, there is a tendency to reject the use of remains from captive animals for morphological studies, assuming their anatomical traits are not representative of the wild morphology (O'Regan, 2001; O'Regan and Kitchener, 2005). Environmental conditions, including dietary habits, substrate composition or climatic constraints, certainly differ between captive-bred and wild animals (Perkins, 1992; Morgan and Tromborg, 2007) but it is not well known yet whether such differences have a direct impact on bone morphology (Zuccarelli, 2004). Several morphological studies have attempted to understand the influence of captivity on bone morphology, although most of them have focused on cranial differences in mammalian species, such as felines (Hollister, 1917; O'Regan, 2001; Zuccarelli, 2004) or Asian rhinoceros (Groves, 1982), and none has yet considered the effects of captivity on morphology of postcranial bones in great apes. Wild great apes perform a great variety of locomotor behaviors, facilitated by the great mobility of their glenohumeral joint that allows free overhead elevation of the arm in the scapular plane (Roberts, 1974; Larson, 1993). These locomotor differences have been directly linked with differences in the morphology of the scapular blade, fossae and spine (Roberts, 1974; Young, 2008; Bello-Hellegouarch et al., 2013). The scapula is the forelimb bone that varies most in shape among primates (Oxnard, 1967) due to the strong relationship between its morphology and function of the shoulder muscles during locomotion (Inman et al., 1944; Ashton and Oxnard, 1963; Oxnard, 1967, 1968, 1969; Oxnard and Neely, 1969; Roberts, 1974; Shea, 1986; Larson and Stern, 1986, 1987, 1989, 1992; Larson et al., 1991; Larson, 1993, 1995; Green et al., 2012).

The behavior of captive great apes is conditioned by a variety of factors, including the spatial limitations and

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TABLE 1. Number of specimens analyzed by species, origin (captive, wild) and sex

	Captive ($N = 30$)		Wild ($N = 27$)		
Species	Male	Female	Male	Female	Unknown
Gorilla gorilla	5	6	4	1	0
Pan troglodytes	6	6	5	7	1
Pongo pygmaeus	1	6	5	4	0
All	12	18	14	12	1

TABLE 2. Type (Bookstein et al., 1999; O'Higgins, 2000) and description of landmarks used in the GM analysis.

Landmark	Type	Name/definition
1	Type II	Suprascapular notch
2	Type II	Superior angle of the scapula
3	Type I	Intersection between vertebral border and base of scapular spine
4	Type II	Spinoglenoid notch
5	Type I	Intersection point of the teres major fossa and the vertebral border of the scapula
6	Type II	Inferior angle of the scapula
7	Type II	Lateral expansion of the teres major fossa
8	Type I	Intersection point of the teres major fossa and the lateral border of the scapula
9	Type II	Infraglenoid tubercle

structure of the enclosures they live in (Kimes et al., 1981; Wilson, 1982; Perkins, 1992; Hosey, 2005), frequently lacking natural stimuli, which can result in a variety of physical and psychological problems (Clarke et al., 1982; Birkett and Newton-Fisher, 2011), affecting their locomotor and postural behaviors. Although in recent years mammals, and in particular primates, receive regular environmental enrichment devices to alleviate the lack of stimulation (Clarke et al., 1982; Rumbaugh, 1982; Perkins, 1992; Robinson, 1998; Hebert and Bard, 2000), even the best naturalized zoological environments are still very limiting and some abnormal behaviors persist (Clarke et al., 1982; Birkett and Newton-Fisher, 2011). In this study, we aimed to assess if captivity conditions have a measurable impact on scapular shape morphology of extant great apes from zoological facilities compared to that of wild populations. Our intention was not to debate the pros and cons of captivity, but rather to evaluate the usefulness of the scapula of captive specimens for making anatomical and locomotor inferences of the species as a whole. Thus, shape differences on the dorsal side of the scapula between captive and wild specimens of some Hominidae species were analyzed with a landmark-based geometric morphometrics (GM) procedure.

MATERIAL AND METHODS

The scapulae of 57 Hominidae primate specimens were analyzed (Table 1). The remains were curated at three institutions: the Museum of Natural Sciences in Barcelona, Spain ($N = 14$); the Anatomical Museum of the University of Valladolid, Spain ($N = 16$); and the Smithsonian National Museum of Natural History in Washington, DC ($N = 27$). Neither the cause of death nor the age at death of these specimens was available for most of both the wild and captive specimens, though all of the analyzed specimens were classified as adults based on dental eruption patterns. The specimens studied (Table 1) included three Hominoidea species: *Gorilla gorilla* ($N = 16$; 11 captive, 5 wild); *Pan troglodytes* ($N = 25$; 12 captive, 13 wild); and *Pongo pygmaeus* ($N = 16$; 7 captive, 9 wild). All the specimens from the Smithsonian Natural History Museum were wild-caught animals and served as comparative controls to the captive ones that came from various Spanish zoos and institutions (zoological parks in Barcelona, Madrid, Matapozuelos in Valladolid, Santillana in Santander, Loro Park in Tenerife, Bioparc in Valencia and Fundació MONA in Girona). Detailed information on the provenance of all captive specimens (N=30) was not available, though. A total of 17 specimens (4 gorillas, 7 chimpanzees and 6 orangutans) were born in captivity and 6 (4 gorillas and 2 chimpanzees) were wild caught as juveniles, as was the case for the well-known gorilla *Copito de Nieve* that spent the rest of his life in captivity. No specific information was available for the other 7 specimens (3 gorillas, 3 chimpanzees and 1 orangutan), some of which were seized by the police from their owners and then brought to public institutions, as documented for two chimpanzees from MONA that had formerly lived under deplorable conditions for years. Despite the fact that Spanish zoological institutions have greatly improved in the last decades, captive Hominoidea suffer great mobility limitation, both from the reduced size of their enclosures and the little time they spend in locomotor activities similar to those practiced in natural environments.

Following the GM nomenclature by Bookstein (1991), nine anatomical operationally homologous landmarks representative of scapular shape (Bello-Hellegouarch et al., 2013) were considered (Table 2, Fig. 1). Since scapulae are not perfectly flat, some dimensions may be distorted when representing 3D objects in a two-dimensional plane. To minimize this, digital images were obtained with a Canon EOS 550D camera, keeping the focal distance constant and with the scapulae oriented with the plane defined by landmarks 3, 4, and 5 parallel to the plane of focus. The distortion caused by projecting all landmarks onto this plane has been shown to have its greatest effect on the acromion (Swiderski, 1993), not considered in our analysis. The coordinates of the landmarks were recorded with tpsDig 2.16 software (Rohlf, 2010) and MorphoJ 1.02 (Klingenberg, 2010) was used to conduct the General Procrustes analysis, a procedure that superimposes all specimens minimizing spatial variability and removing the effects size and orientation of landmark coordinates (Bookstein, 1991; Dryden and Mardia, 1998; Zelditch et al., 2004; Klingenberg, 2010). The resulting dataset, known as Procrustes residuals, was used for multivariate statistical analyses (Rohlf and Marcus, 1993; Bookstein, 1991; Dryden and Mardia, 1998; Zelditch et al., 2004; Klingenberg, 2010).

A principal components analysis (PCA) of scapular shape was performed to visualize patterns of variation within and among groups. PCA reduces complex multidimensional data to a few components or eigenvectors (Zelditch et al., 2004; Klingenberg, 2010; O'Higgins, 2010) that can be used to explain shape differences between groups. The principal component scores were

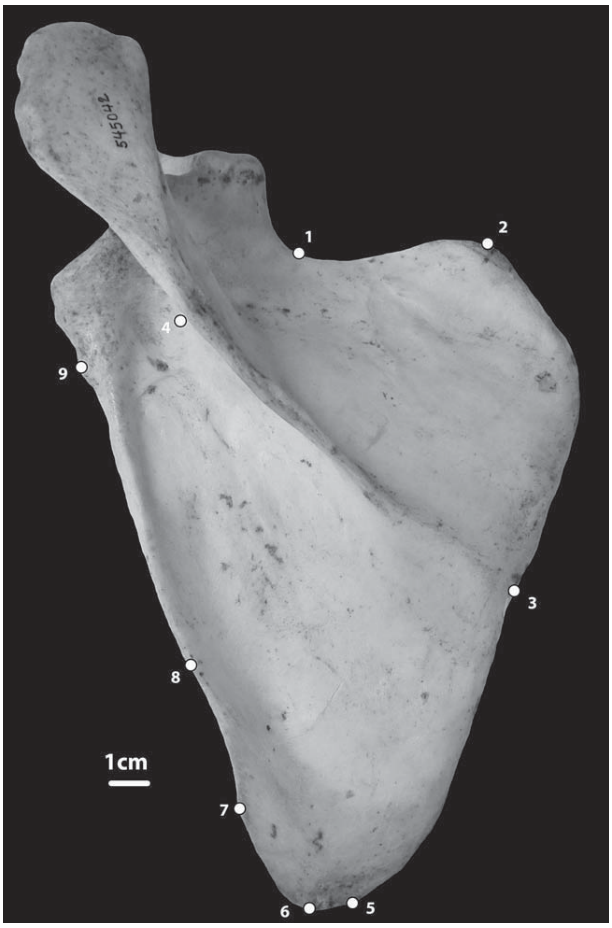

Fig. 1. Dorsal view of the scapulae of *Gorilla* with the landmarks used in the GM analysis.

used in a factorial multivariate analysis of variance (MANOVA) in SPSS (SPSS, Chicago, IL) to test if the differences observed between captive and wild specimens were significant. A *post-hoc* pair-wise comparison (*T*-test) with 1,000 permutations was then performed in MorphoJ from the Mahalanobis and Procrustes distances, and deformation wireframes were drawn to compare mean scapular shapes between captive and wild specimens.

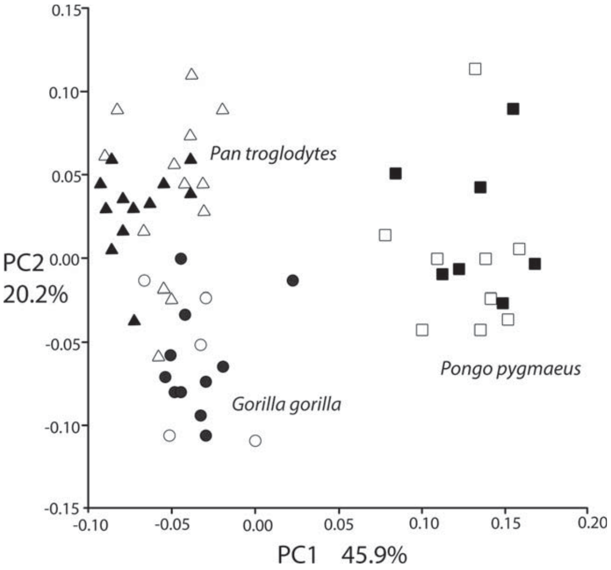

Fig. 2. Scatterplot showing the dispersion of the three studied species (*Gorilla gorilla*, *Pan troglodytes* and *Pongo pygmaeus*) for PC1 vs. PC2, showing the overlapping wild (open symbols) and captive (filled symbols) specimens.

RESULTS

The PCA yielded 14 principal components (PCs) derived from the Procrustes residuals, the first three of which explained 78.7% of total scapular shape variation (45.9% PC1, 20.2% PC2, 12.6% PC3). The scatterplot of the dispersion of the specimens for PC1 vs. PC2 (Fig. 2) showed a clear separation of *Pongo pygmaeus* from *Pan troglodytes* and *Gorilla gorilla* for PC1, and PC2 clearly distinguished *P. troglodytes* from *G. gorilla*. The captive and wild individuals within each species visibly overlapped for these two components. The clear separation of species shown in Figure 2 (representing overall shape variation) was confirmed with the MANOVA test that was highly significant ($F = 6.41$, $P < 0.0005$; Wilk's Lambda=0.003). In addition, the pair-wise comparisons with 1,000 permutations showed that scapular shape differences were significant between species but not between captive and wild individuals within each species (Table 3). The wireframes representing the mean scapular shapes of both captive and wild specimens also showed the lack of morphological differences between the two groups (Fig. 3). Since no differences between captive and wild individuals were found, additional pair-to-pair *post-hoc* T-tests were made between species with wild and captive samples combined, which showed similar significant differences between the three species (Table 4).

DISCUSSION

Our GM analysis detected significant differences in scapular shape among species, both for captive and wild groups separated or pooled, consistent with previous GM studies (Young, 2008; Bello-Hellegouarch et al., 2013). *Pongo* showed a distinct scapular shape from those of *Gorilla* and *Pan* that more closely resembled each other, although the two African apes also showed distinct scapular shapes. On the other hand, no significant differences between wild-caught and captive-bred specimens were observed for all the species analyzed, which suggests that captivity might have not significantly affected scapular shape morphology. If this can be shown also for other osteological collections, captive specimens might be considered in morphological analyses as representative of wild specimens. However, our results cannot necessarily be extrapolated to other skeletal features, since different bones may respond in dissimilar ways to the same external stimuli (Biewener and Gillis, 1999; Pearson and Lieberman, 2004; Plochocki et al., 2008; Green et al., 2012), as observed in the ulna of *Pithecia pithecia* caused by the forced quadrupedal activities performed by the animal due to the small size of their cages (Fleagle and Meldrum, 1988). In this regard, geometric morphometrics seems to be a useful tool to assess the impact of captivity in bone morphology and it would therefore be interesting to perform this kind of analysis in other

TABLE 3. Mahalanobis and Procrustes (in italics) distances found within each locomotor group depending on the wild or captive origin of the individuals, with P-values (in parenthesis) of the T-tests based on 1000 permutations

		Gorilla gorilla		*Pan troglodytes*		*Pongo pygmaeus*
		Captivity	Wild	Captivity	Wild	Captivity
G. gorilla	Captivity ($N=11$)	–				
	Wild ($N=5$)	30.47 (0.2180)	–			
		0.03 (0.9150)	–			
P. troglodytes	Captivity ($N=12$)	8.33 (0.0010)	14.09 (0.1310)	–		
		0.11 (<0.0001)	*0.11 (0.0010)*	–		
	Wild ($N=13$)	6.76 (<0.0001)	20.88 (0.0160)	3.19 (0.1340)	–	
		0.12 (<0.0001)	*0.11 (0.0010)*	*0.05 (0.0160)*	–	
P. pygmaeus	Captivity ($N=7$)	12.50 (0.0480)	10.40 (<0.0001)	13.90 (0.0100)	22.92 (<0.0001)	–
		0.19 (<0.0001)	*0.19 (<0.0001)*	*0.21 (<0.0001)*	*0.19 (<0.0001)*	–
	Wild ($N=9$)	14.69 (0.0010)	10.73 (0.0510)	14.33 (<0.0001)	14.88 (<0.0001)	7.41 (0.6340)
		0.18 (<0.0001)	*0.18 (0.0010)*	*0.21 (<0.0001)*	*0.18 (<0.0001)*	*0.06 (0.2300)*

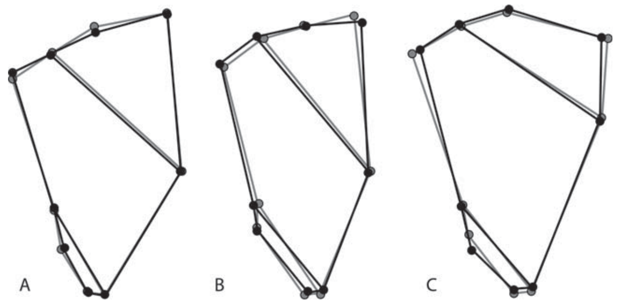

Fig. 3. Shape changes between group centroids. Comparisons shown correspond to: shape changes between wild (black) and captive (gray) for *Gorilla* (**A**), *Pan* (**B**), and *Pongo* (**C**).

TABLE 4. Mahalanobis and Procrustes (in italics) distances found within each locomotor group (captive and wild individuals all together), with P-values (in parenthesis) of the T-tests based on 1000 permutations

	Gorilla gorilla ($N=26$)	*Pan troglodytes*
Pan troglodytes ($N=25$)	5.56 (<0.0001)	
	0.11 (<0.0001)	
Pongo pygmaeus ($N=16$)	9.03 (<0.0001)	10.84 (<0.0001)
	0.18 (<0.0001)	*0.19 (<0.0001)*

postcranial elements to accurately identify if captivity conditions may differentially affect various anatomical areas.

Additionally, we cannot discount that captivity conditions might affect shoulder muscles while bone morphology is preserved, since these are more susceptible than bones to the different habitat conditions and behavioral differences (Ward and Sussman, 1979). Comparing the shoulder musculature of captive-bred and wild-caught Hominidae would certainly be informative. Some studies on the shoulder musculature of the Hominoidea (Potau et al., 2009; Myatt et al., 2012) have been made, as well as of model organisms such as mice (Green et al., 2012), but data from animals in natural habitats are lacking due to the difficulties and ethical issues involved.

CONCLUSIONS

No significant differences in scapular shape were found between captive-bred and wild-caught Hominidae primates, which suggest that captivity may not significantly influence the scapular morphology of extant great apes. The scapulae of the captive specimens analyzed can, thus, be used in morphological or taxonomic analyses, alone or along with those of wild-caught specimens, since they do not represent atypical specimens unrepresentative of the wild morphology.

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4. Two-dimensional geometric morphometric analysis of the anatomical adaptations to locomotor behaviors of pronograde primates in the dorsal side of the scapula.

Bello-Hellegouarch G, Potau JM, Arias-Martorell J, Pastor JF, Pérez-Pérez A.

En revisión.

RESUMEN

Numerosos estudios se han centrado en la relación entre la morfología de la escápula y los comportamientos locomotores de los primates (Roberts 1974; Taylor & Slice 2005; Young 2006, 2008; Green *et al*. 2012). Sin embargo, la mayoría de ellos o bien se centran en la escápula de los primates ortógrados o emplean medidas anatómicas como herramientas para discriminar grupos locomotores, sin profundizar en cuáles son las razones funcionales que explican esas diferencias. En este estudio se analiza la relación entre los patrones locomotores de los primates pronógrados (incluyendo haplorrinos y estrepsirrinos) y la morfología de la cara dorsal de la escápula, asociando cada categoría locomotora a una forma escapular específica con el fin de comprender los requerimientos anatómicos asociados con el modo de locomoción particular de cada taxón. Se analiza la influencia de la locomoción sobre la morfometría geométrica 2D de la cara dorsal de la escápula mediante regresiones multivariadas con el fin de identificar la forma asociada a cada categoría locomotora.

El análisis mostró una clara asociación entre los diversos modos de locomoción (cuadrupedia terrestre, cuadrupedia arbórea, cuadrupedia semiterrestre, suspensión bimanual, suspensión cuadrúpeda, *pronograde clambering*, *slow-climbing quadrupedalism*, *leaping*, *vertical clinging and leaping*, *vertical clinging*) y las formas escapulares asociadas a ellos. El tamaño relativo de las fosas supraespinosa e infraespinosa y el área de inserción del músculo redondo mayor mostraron patrones de diversidad asociados a factores funcionales y adaptaciones anatómicas de cada tipo de locomo-

ción. Algunos primates requieren una mayor estabilización de la articulación glenohumeral, mientras que otros requieren mayor movilidad para poder alcanzar las ramas altas de los árboles, y estos requisitos diferentes se ven reflejados en el tamaño de las fosas supraespinosa e infraespinosa.

Two-dimensional geometric morphometric analysis of the anatomical adaptations to locomotor behaviors in the dorsal side of the scapula of pronograde primates

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ABSTRACT

Scapular shape in primates is highly related to the function of the muscles that insert on the scapula or originate from it, especially in the case of the rotator cuff muscles. The scapular's shape is considered to strongly reflect the animals' diverse locomotor modes and behaviors. Ortograde primates (hominoids) have been well studied, but thorough study of the locomotor and anatomical adaptations in the scapulae of pronograde primates is still lacking. For this purpose we conducted a two-dimensional geometric morphometric analysis of the dorsal side of the scapula in 33 species of pronograde primates that use different locomotor modes. We extracted the shape associated with each mode and explained it in terms of anatomical and functional adaptations to better understand the requirements associated with each locomotor strategy. We found that each locomotor mode has specific requirements that are reflected in the scapular shape. However, since all species use more than one type of locomotion, their scapular shape will reflect a compromise between the requirements of distinct locomotor modes.

INTRODUCTION

Primates comprise the most diverse mammalian order with regard to postcranial morphology and positional behavior [Cant 1992; Cant et al., 2001; Garber 2007], characteristics that underlie their successful radiation in tropical forests. This radiation reflects the different ways in which species exploit three-dimensional habitats [Garber 2007; Nowak 1999], which resulted in a large number of locomotor specializations. Consequently, it is very difficult to assign primate species to a single locomotor category, and considerable discussion exists in the literature about behavioral categorization possibly being more precise [Hunt et al., 1996; Napier & Napier 1967; Prost 1965; Rose 1973; Wright-Fitzgerald et al., 2010]. Although broad locomotor categories are imprecise and do injustice to the actual diversity of primate movements [Ankel-Simons 2007; Fleagle 1999], they are often used to facilitate the categorization and posterior analysis of data, based upon the frequency of time spent in a given behavior [Wright-Fitzgerald et al., 2010]. Locomotion in most primate species tends to depend on the animals' body size, their diet, the substrate they use, the climate, forest types, and the height of the canopy in which the primates spend most of their time [Ankel-Simons 2007; Charles-Dominique 1990; Fleagle 1999; Nowak 1999]. Therefore, primate species can be generally assigned the following nonexclusive forms of locomotion: arboreal quadrupedalism, terrestrial quadrupedalism, climbing, pronograde clambering, leaping, vertical clinging, and/or suspension (e.g., quadrupedal suspension, arm-swinging, brachiation) [Ankel-Simons 2007; Fleagle 1999; Hunt et al., 1996; Nowak 1999; Schmidt 2010].

Arboreal quadrupedalism, the progression in a small branch setting using all four limbs [Fleagle 1999; Rose 1973; Schmidt 2010], is the most common form of locomotion among living primates and probably the ancestral locomotor mode of the earliest species [Fleagle 1999; Martin 1990; Nowak 1999; Rose 1973; Schmidt 2010; Schmitt 2003]. Arboreal quadrupeds have to deal with substrates that are discontinuous, mobile, cylindrical in shape, and variable in angulation, size, and weight-bearing capacity, and they share adaptations for maintaining balance and support on relatively small and unstable branches [Cant 1992; Cartmill 1974; Cartmill & Milton 1977; Dunbar & Badam 2000; Garber 2007; Grand 1984]. Different species perform arboreal quadrupedalism in various ways. For example, the locomotion is extremely slow and deliberate in lorises and is known as *slow climbing quadrupedalism*, *tardigrady*, or *lorisine crawling*, a progression that typically involves the movement of only one limb at a time [Demes et al., 1990; Gebo 1987, 1989; Hunt et al., 1996; Jouffroy 1989; Napier & Napier 1967; Runestad 1997; Schmidt 2010; Walker 1974]. *Pronograde clambering* or *scramble* consists of above-substrate quadrupedal progression that lacks a regular gait and occurs across multiple and irregular placed supports of different sizes and angles; this locomotion is typical of howler monkeys [Cant et al., 2001; Hunt et al., 1996; Schön Ybarra 1987]. *Terrestrial quadrupedalism* is relatively rare among primates and is characteristic of large Old World monkeys [Fleagle 1999; Schmidt 2010], which show adaptations related to feeding and progression on the ground that occurs on comparatively uniform and stable substrates and features more continuous pathways to travel [Fleagle 1999; Garber 2007; Rose 1973]. A specialized mode of terrestrial quadrupedalism is *knuckle-walking*, which is seen in the African great apes [Doran 1996; Fleagle 1999; Hunt 1992; Hunt et al., 1996]. *Climbing* is a locomotor mode omnipresent in living primate species that allows ascent or descent on vertical or steeply inclined arboreal supports [Gebo 1996; Hunt et al., 1996; Mittermeier & Fleagle 1976; Schmidt 2010]. *Leaping* is the fastest mode of progression and is usually performed for predator avoidance or for crossing gaps in the forest matrix [Fleagle 1999; Hunt et al., 1996; Nowak 1999; Schmidt 2010]. Leaping consists of covering distances between inclined, vertical, or horizontal substrates in free flight by rapid extension of the hind limbs [Ankel-Simons 2007; Schmidt 2010]. Adaptations for this form of locomotion evolved independently in a number of primate species [Fleagle 1999; Nowak 1999; Terranova 1996] and are highly specialized in the small-sized galagos and tarsiers. These species progress by *vertical-clinging* and *leaping*, which are characterized by surprisingly long jumps in a partially upright position that are powered mainly by the hind limbs [Gebo 1987; Hunt et al., 1996; Napier & Walker 1967; Walker 1974]. Vertical-clinging and leaping done by prosimians differs from the *vertical-clinging* performed by several small New World monkeys, such as marmosets and tamarins [Ankel-Simons 2007; Hunt et al., 1996; Schmidt 2010], which use their claws to cling to large branches and vertical tree trunks [Ankel-Simons 2007; Garber 1992]. *Quadrupedal suspension* is characterized by horizontal movement below a substrate in an inverted (dorsal-side down) position using all four limbs in tension, typical of lorisids [Fujiwara et al., 2011; Hunt et al., 1996; Napier 1967]. *Bimanual suspension*, such as *arm-swinging* and *brachiation* (mostly distinguished by little and extensive trunk rotation, respectively), is characterized by the bimanual progression beneath a support, allowing larger species to spread their body weight over small supports [Fleagle 1999; Hunt et al., 1996; Jenkins et al., 1978; Jungers & Stern 1981; Mittermeier & Fleagle 1976; Cant et al., 2003]. This locomotor mode is performed by only a few primate species, such as hominoids (specially hylobatids), spider monkeys, and to a lesser extent, woolly monkeys. The suspensory New World monkeys frequently swing from branch to branch by their arms, but unlike apes, they use their prehensile tail as a fifth limb during traveling [Cant et al., 2001, 2003; Hunt et al., 1996; Kagaya 2007; Schmidt 2010].

Primate locomotor evolution is characterized by dramatic changes in the functional role of the forelimbs, which became less important in weight-bearing and support roles as their mobility and ability to provide stability, grasping, and manipulation in a discontinuous arboreal environment increased [Larson 1998; Lemelin & Schmitt 2007; Rose 1973; Schmitt 1998, 2010; Schmitt & Lemelin 2002]. In this context, the main role of the shoulder has been to provide the mobility required to reach the irregular supports within the discontinuous arboreal substrate, while keeping the glenohumeral joint adequately stabilized to secure postural stability [Larson 1993; Roberts 1974; Schmidt & Krause 2011]. The scapula is the bone connecting the upper limb to the thorax, and it is largely suspended by muscles, hence its great mobility [Jenkins 2009]. Its morphology is largely determined by the function of the musculature of the glenohumeral joint during locomotion; the muscles in this joint move and stabilize scapular motion and transmit the bodyweight onto the forelimbs [Ashton et al., 1976; Inman et al., 1944; Larson 1993, 1995; Oxnard 1967, 1977; Roberts 1974; Schmidt & Krause 2011]. Among the glenohumeral joint muscles, the rotator cuff muscles (subscapularis, supraspinatus, infraspinatus, and teres minor) play a particularly significant role in the movement and stabilization of the joint in primates [Ashton & Oxnard 1963; Bello-Hellegouarch et al., 2013a; Inman et al., 1944; Larson 1993, 1995; Larson & Stern 1986, 1987, 1989, 1992; Larson et al., 1991; Oxnard 1967, 1968, 1969; Oxnard & Neely 1969; Potau et al., 2009; Roberts 1974; Shea 1986; Wolffson 1950].

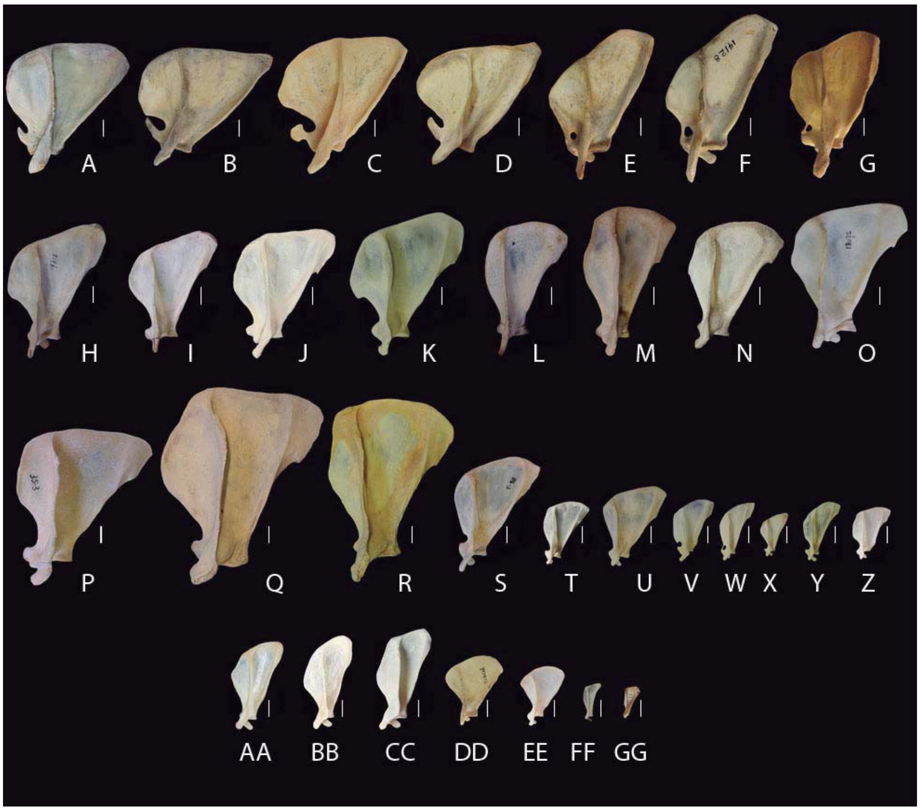

Figure 1. *Dorsal view of the scapulae of the pronograde primates analyzed in this study. Scapulae are oriented so that the length of the scapular spine is perpendicular to the horizontal base. A:* Alouatta caraya*, B:* Alouatta palliata*, C:* Alouatta seniculus*, D:* Alouatta villosa*, E:* Ateles fusciceps*, F:* Ateles geoffroyi*, G:* Lagothrix lagothricha*, H:* Cercopithecus ascanius*, I:* Cercopithecus mitis*, J:* Cercopithecus neglectus*, K:* Colobus guereza*, L:* Chlorocebus aethiops*, M:* Erythrocebus patas*, N:* Macaca fascicularis*, O:* Macaca mulatta*, P:* Macaca sylvanus*, Q:* Mandrillus sphinx*, R:* Papio hamadryas*, S:* Cebus capucinus*; T:* Saimiri sciureus*, U:* Pithecia pithecia*, V:* Callithrix jacchus*, W:* Callithrix penicillata*, X:* Cebuella pygmaea*, Y:* Leontopithecus rosalia*, Z:* Saguinus midas*, AA:* Lemur catta*, BB:* Eulemur fulvus*, CC:* Varecia variegata*, DD:* Nycticebus coucang*, EE:* Perodicticus potto*, FF:* Galago senegalensis*, GG:* Tarsius bancanus*.*

Many studies have compared primate scapulae to better understand the relationship between scapular shape and locomotor function [Ashton & Oxnard 1963, 1964; Ashton et al., 1965; Bello-Hellegouarch et al., 2013a; Corrucini & Ciochon 1976, 1978; Frey 1923; Green et al., 2012; Inman et al., 1944; Inouye & Shea 1997; Inouye & Taylor 2000; Larson 1993, 1995; Larson & Stern 1986, 1987, 1989, 1992; Larson et al., 1991; Oxnard 1967, 1968, 1969; Oxnard & Neely 1969; Roberts 1974; Schultz 1930; Shea 1986; Taylor 1997; Taylor & Slice 2005; Young 2006, 2008]. The morphology of the dorsal side of the scapula has been shown to be strongly related to functional differences, specifically the overall scapular blade shape; the supraspinous and infraspinous fossae shapes, and their sizes and ratios; the teres major fossae; and the spine length and orientation [Bello-Hellegouarch et al., 2013a; Frey 1923; Green et al., 2012; Inman et al., 1944; Roberts 1974; Schultz 1930]. Although primates show a continuous spectrum of scapular shapes (Figure 1), a morphological dichotomy can be defined from among them. Quadrupedal primates (both arboreal and terrestrial) have scapulae that function mostly in retractive-propulsive movements within a restricted parasagittal plane, and these animals tend to have long (extending from the vertebral border to the glenoid fossa) and narrow (from the superior to the inferior angles) blades, with the spine perpendicular to the vertebral border [Larson 1993; Roberts 1974; Schmidt & Krause 2011; Young 2008]. Suspensory primates tend to have short and broad scapulae, with both supraspinous and infraspinous fossae enlarged, and the spine is highly inclined, allowing greater mobility and use of the forelimb above the head [Larson 1993; Roberts 1974; Schmidt & Krause 2011; Young 2008]. However, some variability exists even within groups with the same locomotor patterns because the scapular shape is also influenced to some extent by other factors, such as phylogeny, substrate habitation, or body mass [Anapol et al., 2005; Charles-Dominique 1990; Crompton et al., 1987; Larson 1993; Roberts 1974; Schmidt & Krause 2011; Young 2008].

Table 1. *Species included in the study, including their sex and their family.*

Species	**Male**	**Female**	**Total**	**Family**
Alouatta caraya	4	3	7	Atelidae
Alouatta palliata	13	11	24	Atelidae
Alouatta seniculus	4	5	9	Atelidae
Alouatta villosa	3	1	4	Atelidae
Ateles fusciceps	2	4	6	Atelidae
Ateles geoffroyi	2	5	7	Atelidae
Callithrix jacchus	9	1	10	Callitrichidae
Callithrix penicillata	5	5	10	Callitrichidae
Cebuella pygmaea	6	3	9	Callitrichidae
Cebus capucinus	3	1	4	Cebidae
Cercopithecus ascanius	4	1	5	Cercopithecidae
Cercopithecus mitis	4	3	7	Cercopithecidae
Cercopithecus neglectus	3	5	8	Cercopithecidae
Chlorocebus aethiops	1	3	4	Cercopithecidae
Colobus guereza	2	3	5	Cercopithecidae
Erythrocebus patas	4	3	7	Cercopithecidae
Eulemur fulvus	4	3	7	Lemuridae
Galago senegalensis	5	1	6	Galagidae
Lagothrix lagothricha	4	5	9	Atelidae
Lemur catta	3	5	8	Lemuridae
Leontopithecus rosalia	3	1	4	Callitrichidae
Nycticebus coucang	7	3	10	Lorisidae
Macaca fascicularis	5	2	7	Cercopithecidae
Macaca mulatta	4	2	6	Cercopithecidae
Macaca sylvanus	1	4	5	Cercopithecidae
Mandrillus sphinx	4	3	7	Cercopithecidae
Papio hamadryas	6	1	7	Cercopithecidae
Pithecia pithecia	3	1	4	Pitheciidae
Perodicticus potto	2	4	6	Lorisidae
Saguinus midas	6	5	11	Callitrichidae
Saimiri sciureus	3	4	7	Cebidae
Tarsius bancanus	2	2	4	Tarsiidae
Varecia variegata	2	3	5	Lemuridae
Total	133	106	239	

In this study we examined the relationship between the locomotor patterns of pronograde primates (including Catarrhini and Strepsirrhini species) and the morphology of the dorsal side of their scapulae. Our aim was to associate each locomotor category to a specific scapular shape to better comprehend the anatomical requirements of each particular mode of locomotion. We conducted a two-dimensional (2D) geometric morphometric analysis of the dorsal side of the scapula of multiple pronograde primate species with different locomotor patterns. We performed multivariate regressions on the scapular shapes for the different locomotor modes to determine the influence of locomotion on the scapular shape and to identify the shape associated with each locomotor category. Our analysis also included several biological and ecological factors that have been reported to influence the forelimb bone morphology, such as phylogeny, body mass, scapular size, and canopy-level preference.

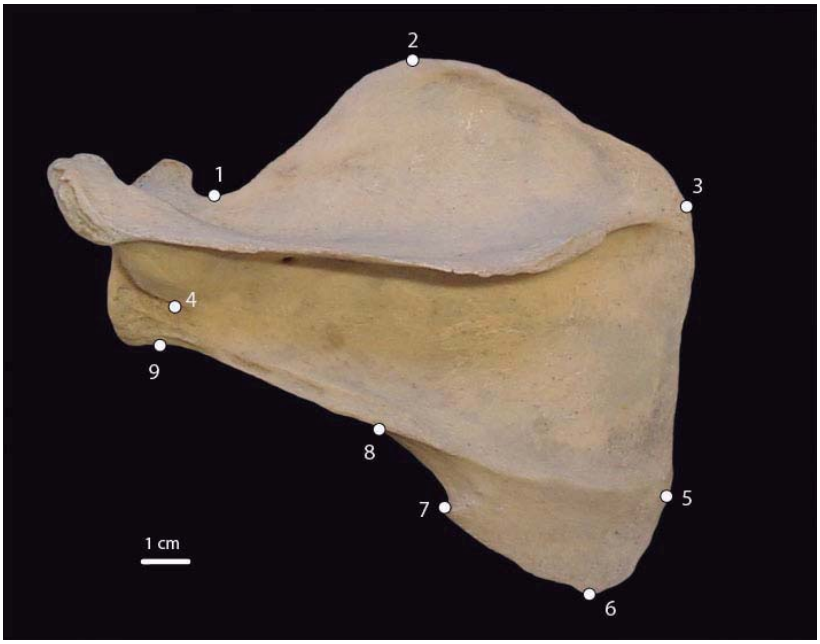

***Figure 2**. Landmarks used in the GM analysis shown in the scapula of* Mandrillus sphinx*.*

METHODS

The scapulae of 239 pronograde primate specimens (Table 1, Figure 1) were analyzed, using samples from four institutions: the Museum of Natural Sciences, Barcelona, Spain (N=27); the Anatomical Museum of the University of Valladolid, Spain (N=85); the Royal Institute of Natural Sciences in Brussels, Belgium (N=47); and the Smithsonian Institution National Museum of Natural History, Washington DC (N=80). All specimens were from adults of unknown age at death. Since it has been suggested that captivity does not have a significant impact on scapular morphology [Bello-Hellegouarch et al., 2013b], we used specimens from both captive and wild individuals.

We defined nine anatomical landmarks (Table 2, Figure 2) on 2D digital images of the scapular blades. We oriented the scapulae with the plane defined by landmarks 3, 4, and 5 parallel to the plane of focus and kept the distance to the digital camera constant to avoid the distortion caused by representing nonflat three-dimensional objects in two dimensions [Swiderski 1993]. The distortion would have its greatest effect on the acromion, which did not affect our analysis. After obtaining the digital images with a Canon EOS 550D digital camera, we recorded the coordinates of the landmarks with tpsDig 2.16 software [Rohlf 2010]. The landmarks were considered operationally homologous and representative of overall scapular shape and supraspinous, infraspinous, and teres major fossae shape [Ashton & Oxnard 1964; Ashton et al., 1976; Bello-Hellegouarch et al., 2013a, b; Larson 1993, 1995; Oxnard 1967; Roberts 1974; Schultz 1930; Shea 1986; Taylor 1997; Taylor & Slice 2005; Young 2006, 2008;]. We analyzed the infraspinous and teres minor fossae together, since both muscles are lateral rotators of the glenohumeral joint [Larson & Stern 1986, 1987; Tuttle & Basmajian 1978a, 1978b].

Data analysis

A General Procrustes Analysis (GPA) was carried out in MorphoJ [Klingenberg 2010] to remove variability related to position (translation), orientation (rotation), and geometric scale (rescaling) [Bookstein 1991; Dryden & Mardia 1998; Klingenberg 2010; Rohlf 1999; Zelditch et al., 2004]. The resulting GPA-aligned coordinates, now projected into the tangent space, were used in multivariate statistical analyses [Bookstein 1991; Rohlf & Marcus 1993; Dryden & Mardia 1998; Klingenberg 2010; Zelditch et al., 2004].

Table 2. *Type (Bookstein, 1991; O'Higgins, 2000) and description of landmarks used in the GM analysis.*

Landmark	Type	Name / definition
1	II	Suprascapular notch
2	III	Superior angle of the scapula
3	I	Intersection between vertebral border and base of scapular spine
4	II	Spinoglenoid notch
5	I	Intersection point of the teres major fossa and the vertebral border of the scapula
6	III	Inferior angle of the scapula
7	III	Lateral expansion of the teres major fossa
8	I	Intersection point of the teres major fossa and the lateral border of the scapula
9	II	Infraglenoid tubercle

We used the GPA-aligned coordinates to conduct a principal components analysis (PCA) to visualize patterns of variation among species [Klingenberg 2010]. PCA incorporates and reduces complex multidimensional data to a set of eigenvectors [Klingenberg 2010;

O’Higgins 2010; Zelditch et al., 2004]. It also rotates data points to their major axes for better visualization, which preserves original distances between points; the vectors are uncorrelated, and each is ordinated in terms of the amount of variance explained [Manly 1994; Neff & Marcus 1980]. We used the PC scores derived from the PCA to make a factorial multivariate analysis of variance (MANOVA) to test the hypothesis that species differ in overall scapular shape. Statistical analyses were done with SPSS (SPSS, Chicago, IL, USA). We then performed pairwise randomizations with 1000 permutations on both the Mahalanobis and Procrustes distances in MorphoJ [Klingenberg 2010] to test for significant differences among the group means.

A series of multivariate regression analyses were conducted to test whether differences in overall shape change were correlated with independent external variables [Frost et al., 2003; Turley et al., 2011]. For this purpose the Procrustes coordinates served as dependent variables, with locomotion, canopy-level preference, body mass, phylogeny at family level, and scapular size as independent variables (further discussed in the next subsection *The external variables*). Although MorphoJ doesn’t allow multiple multivariate regressions (many dependent variables and many independent variables), it permits grouping some independent variables (i.e., the variables related to locomotion) to give a percentage of shape variation related to them as a whole. To understand the impact of locomotion on the dorsal side of the scapula, shape differences associated with each specific locomotor category were visualized in MorphoJ by extracting the landmark configuration related to each particular locomotor shape component [Adams & Nistri 2010; Drake & Klingenberg 2008; Turley et al., 2011].

The external variables. Estimated body mass for all taxa was derived from the literature [Smith & Jungers 1997] since the real body mass of each individual was unknown. The means of the centroid size (CS) were used as estimators for scapular size [Bookstein 1996]. Canopy level preference (CLP), family (FAM, Table 1), and the locomotor behaviors (LOC) were performed by coding these factors as dichotomous ("dummy coded") variables based on presence (1) and absence (0) categories. The LOC variable was divided into 11 categories: bimanual suspension, terrestrial quadrupedalism, arboreal quadrupedalism, semiterrestrial quadrupedalism, slow climbing quadrupedalism, climbing, quadrupedal suspension, pronograde clambering, leaping, vertical-clinging, and vertical-clinging and leaping based on the literature [Anapol et al., 2005; Ankel-Simons 2007; Cant 1988; Cant et al., 2001, 2003; Fleagle 1999; Fleagle & Meldrum 1988; Fleagle & Mittermeier 1980; Fujiwara et al., 2011; Gebo 1987, 1989; Gebo & Chapman 1995; Gebo & Sargis 1994; Hunt et al., 1996; Jouffroy 1989; Napier 1967; Mittermeier & Fleagle 1976; Rose 1973; Schmidt 2010; Schmitt 2010; Terranova 1996; Walker 2005; Ward & Sussman 1979; Youlatos 1999], while the CLP was divided into five categories: emergent, medium canopy, lower canopy, understory, and ground [Ankel-Simons 2007; Fleagle 1999].

RESULTS

We obtained 14 principal components (PCs) from the Procrustes residuals, and the first three explained 71.4% of scapular shape variation (34.8% PC1, 23.2% PC2, 13.4% PC3). Although the scatter plot of PC1 *vs.* PC2 was confusing when all species were considered together, it showed a clear separation among families (Fig. 3a). To facilitate understanding of the distribution of the different species, we include the scatter plot with the families together (Fig. 3a) and the species separately by families (Fig. 3b, 3c, 3d, 3e). The distribution of Atelidae is shown in Figure 3b. The three genera (*Alouatta*, *Ateles*, and *Lagothrix*) had statistically significant differences from one another. The four *Alouatta* species clustered together, sharing the most positive PC1 values. *Lagothrix* showed the most positive PC2 values, while *Ateles* showed a high dispersion along the PC1 axis, overlapping to some extent with *Alouatta*. Figure 3c shows a wide separation among the prosimian families, which was statistically confirmed by the randomization tests, with Galagidae, Lemuridae, and Tarsiidae sharing the highest negative PC1 and PC2 values on one side, and the Lorisidae with the highest positive PC1 and PC2 values on the other side of the plot.

This dispersion makes sense when not only the phylogeny is taken into account, but also when the different locomotor patterns performed by those two distinct groups are considered. This influence of locomotion was also observed in the Cercopithecidae (Fig. 3d), with a slightly gradual separation occurring between the more terrestrial species (e.g., *Erythrocebus patas*) with the most negative PC1 values and the more arboreal ones (e.g., *Colobus guereza*, *Cercopithecus mitis*) with the highest positive PC1 values (while PC2 doesn’t separate species). The Cebidae completely overlapped with them, despite being phylogenetically distant taxa (Fig. 3a). Finally, Figure 3e shows three families: Callitrichidae (*Callithrix jacchus*, *Callithrix penicillata*, *Cebuella pygmaea*, *Leontopithecus rosalia*, *Saguinus midas*), Pitheciidae (*Pithecia pithecia*) and Cebidae (*Cebus capucinus*, *Saimiri sciureus*). Pitheciidae were significantly separated from the other families. All the Callitrichidae overlapped to some extent, except for *Leontopithecus rosalia*, which clearly remained separated from the rest of the family. Furthermore, Callitrichidae overlapped to some extent with Cebidae, Lemuridae, and Cercopithecidae (Fig. 3a).

The separation of species shown in Figure 3 was statistically confirmed by the MANOVA and the pairwise analyses. The MANOVA showed a statistically significant difference in the PC scores (representing the overall shape variation), F(448, 2534)=10.531, P<0.0005; Wilks' lambda=0.000.

The effect on the scapular shape for each factor studied separately was highly significant for all the regressions carried out (P<0.0001). The regression on LOC explained 53.5% of the variance; FAM explained 50.9% of the variance; CLP explained 27.8% of the variance; CS explained 7.3% of the variance (7.6% when considering size and sex together); and BM explained 5.3% of the variance.

Given that this study focused on the influence of the locomotion behavior on the scapular shape, only shape differences associated with the LOC factor were examined (Fig. 4). Since the category *Climbing* is a mode omnipresent in all extant primates, we used the shape associated with this mode as a mean shape to facilitate visualization of those differences observed in the scapular shapes adapted to each of the locomotor categories analyzed here (Fig. 4).

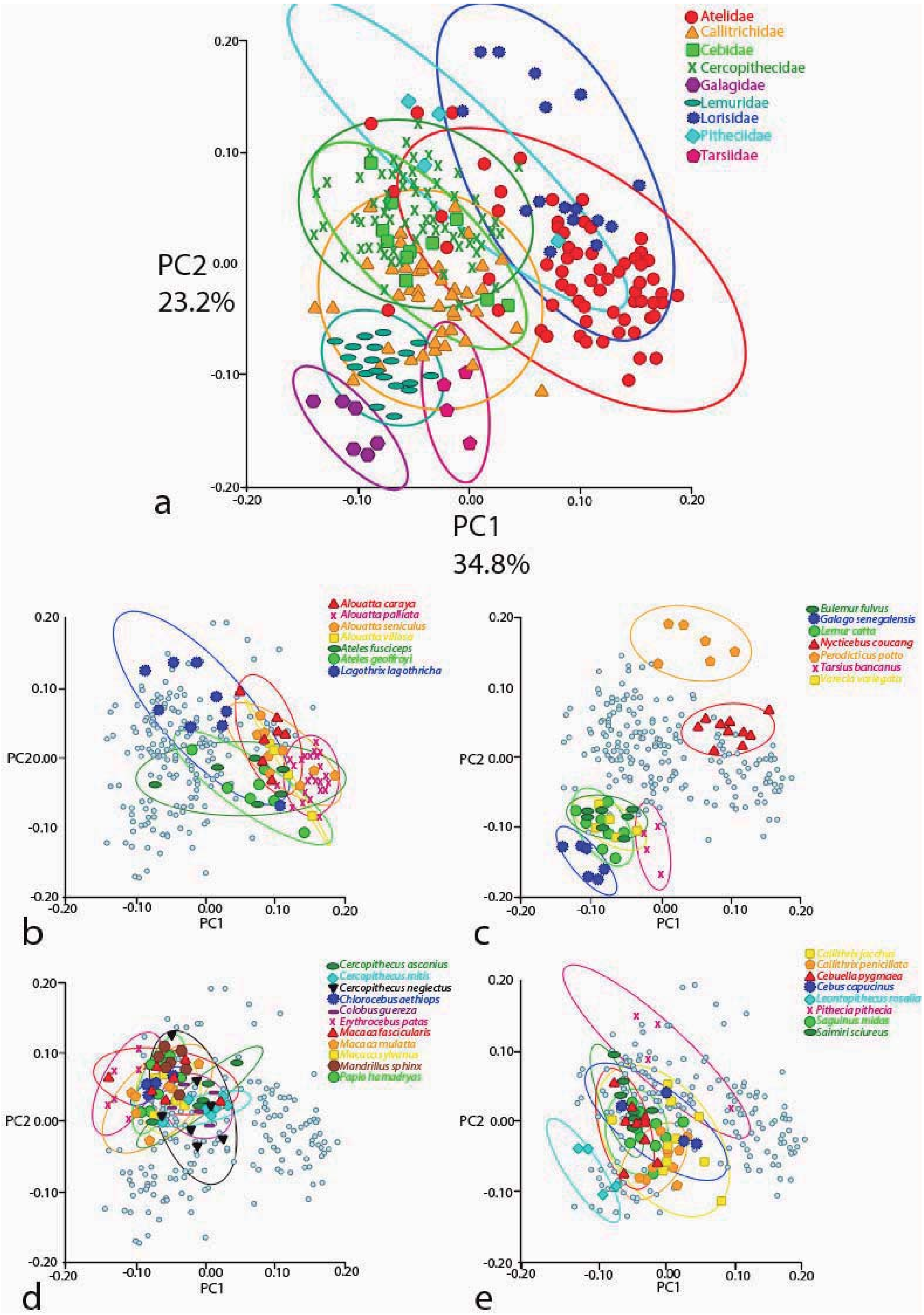

***Figure 3**. Scatterplot of the first two principal components (PC1 and PC2) derived from the PCA of the GM analysis. A: distribution of the nine families included in this study (Atelidae, Callitrichidae, Cebidae, Cercopithecidae, Galagidae, Lemuridae, Lorisidae, Pitheciidae and Tarsiidae); B: detail of the distribution of the seven species of Atelidae analyzed (*Alouatta caraya*, Alouatta*

palliata*,* Alouatta seniculus*,* Alouatta villosa*,* Ateles fusciceps*,* Ateles geoffroyi *and* Lagothrix lagothricha*); C: detail of the distribution of the seven prosimian (Galagidae, Lemuridae, Lorisidae and Tarsiidae) species analyzed (*Eulemur fulvus*,* Galago senegalensis*,* Lemur catta*,* Nycticebus coucang*,* Perodicticus potto*,* Tarsius bancanus *and* Varecia variegata*); D: detail of the distribution of the eleven especies of Cercopithecidae analyzed (*Cercopithecus ascanius*,* Cercopithecus mitis*,* Cercopithecus neglectus*,* Chlorocebus aethiops*,* Colobus guereza*,* Erythrocebus patas*,* Macaca fascicularis*,* Macaca mulatta*,* Macaca sylvanus*,* Mandrillus sphinx *and* Papio hamadryas*); E: detail of the distribution of the five species of Callitrichidae (*Callithrix jacchus*,* Callithrix penicillata*,* Cebuella pygmaea*,* Leontopithecus rosalia *and* Saguinus midas*) and the specie of Pitheciidae (*Pithecia pithecia*) and the two species of Cebidae analyzed (*Cebus capucinus *and* Saimiri sciureus*).*

Arboreal, semiterrestrial, and terrestrial quadrupedalism (AQ, STQ, and TQ; Fig. 4a–4c). The scapular shape related to arboreal, semiterrestrial, and terrestrial quadrupedalism was very similar, characterized by a long and narrow scapula and a long scapular spine. TQ showed a relatively wider supraspinous fossa compared with the infraspinous one (separation of L1 and L4, and L2 and L3) and a longer scapular spine (outward displacement of L3) than the AQ. The STQ showed intermediate sizes, with a slightly wider supraspinous fossa compared with the AQ. The teres major was very similar among the three groups, being slightly smaller in TQ (approximations of L6 towards L7).

Bimanual suspension (BS; Fig. 4d). With regard to bimanual suspension, the scapula was short and wide (inward displacement of L3 and L4). Both infraspinous and supraspinous fossae were broad overall, and the teres major fossa was long and narrow (approximation of L8 towards L9, L7 towards L8, and L6 towards L5).

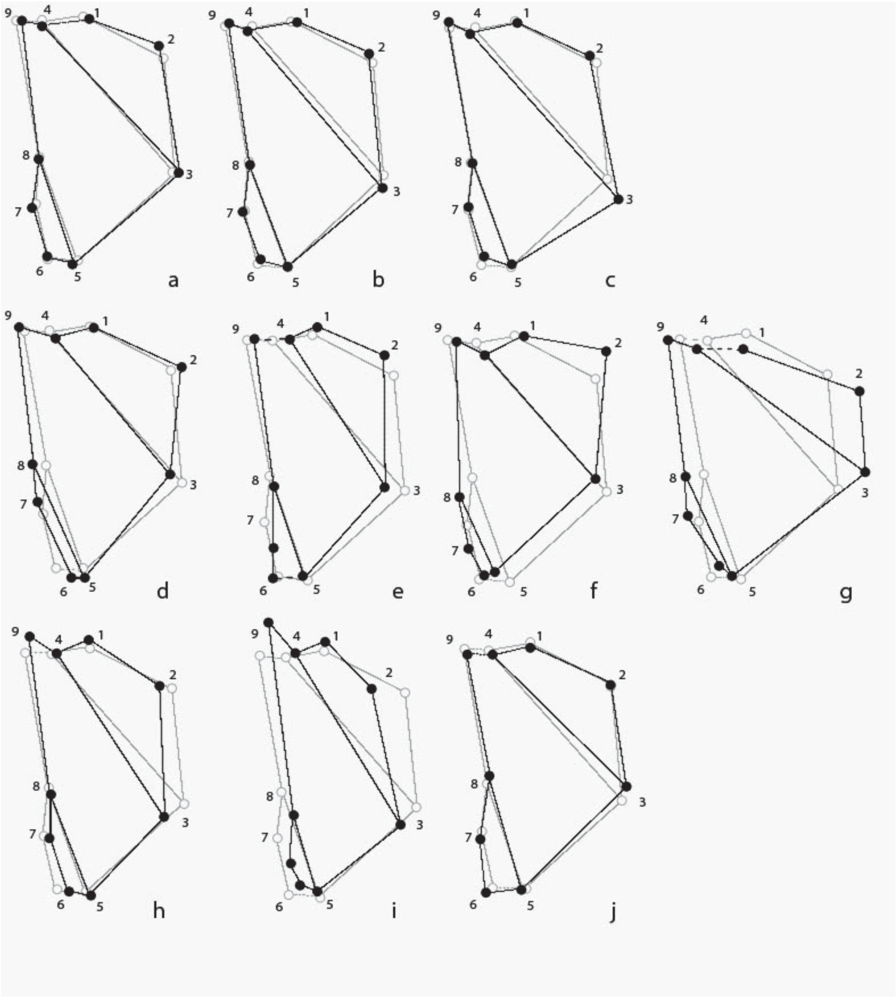

Figure 4. *Scapular shape associated with each particular locomotor modes extracted from the regression analysis. A: arboreal quadrupedalism; B: semiterrestrial quadrupedalism; C: terrestrial quadrupedalism; D: bimanual suspension; E: quadrupedal suspension; F: pronograde clambering; G: slow quadruped climbing; H: leaping; I: vertical-clinging and leaping; J: vertical-clinging. The scapular shape associated with each locomotor mode is displayed in black, while the mean shape related to the Climbing mode is displayed in gray.*

Quadrupedal suspension (QS; Fig. 4e). Quadrupedal suspension was associated with a short and wide scapula, similar to the BS one. Although both infraspinous and supraspinous fossae were broad overall, they were smaller than the BS ones (outward displacement and approximation of L1 and L2; inward displacement of L3), while the teres major fossa was short (approximation of L7 towards L6).

Pronograde clambering (PC; Fig. 4f). Pronograde clambering is characterized by short and wide supraspinous and infraspinous fossae. The spine is shorter than that found with the other locomotor modes (inward displacement of L3 and L4), leading to the shortening of both fossae. The supraspinous fossa was characteristically wide due to the outward displacement of L2. The infraspinous fossa was wide due to the outward displacement of L5 and L8, thereby reducing the teres major fossa size (approximation of L5 towards L6).

Slow-climbing quadrupedalism (SCQ; Fig. 4 g). The overall scapular shape associated with slow-climbing quadrupedalism was characterized by a blade with similar length and width, with a long vertebral border, and an extremely broad infraspinous fossa (outward displacement of L3, L8 and L9) in relation to the supraspinous one, which was less well-developed (approximation of L3 towards L2; inward displacement of L1). The teres major fossa was extremely narrow compared with the scapular shapes related to the remaining locomotor modes (approximation of L5 and L6).

Leaping (L; Fig. 4h). The scapula of generalist leapers was similar to the VCL one, although not so slender. The supraspinous fossa was wider in the less specialized leapers (separation of L2 and L3), while the infraspinous fossa remained similar in both categories. However, the teres major fossa was broader, remaining similar to the one observed in terrestrial quadrupeds.

Vertical clinging and leaping (VCL; Fig. 4i). The overall scapular shape of a vertical-clinger and leaper (such as *Galago* or *Tarsius*) was a long and extremely narrow scapula, with relatively small and narrow supraspinous fossa (inward displacement of L2, and displacement of L4 towards L1). The outward displacement of L9 as well as the displacement of L3 towards L5 led to the narrowing of the infraspinous fossa. The approximation of L5 and L8, as well as the inward displacement of L6 and L7, led to an overall reduction of the teres major fossa.

Vertical-clinging (VC; Fig. 4j). With the vertical-clinging mode, the scapula was characterized by an increase of the infraspinous fossa in relation to the supraspinous one (approximation of L3 towards L2), and a wide teres major fossa (outward displacement of L6 and L7). The infraspinous fossa was wider than it was in quadrupeds, while the supraspinous fossa was relatively narrow.

DISCUSSION

In this study the dorsal side of the scapula was analyzed to understand the requirements associated with the different locomotor modes of pronograde primates. Three of the rotator cuff muscles (supraspinatus, infraspinatus, and teres minor) originate on the dorsal side of the scapula, as does the teres major muscle. The rotator cuff muscles play important roles in the movement and stabilization of the shoulder joint, and consequently their different patterns of recruitment are strongly related to locomotor behaviors and the differential use of the scapula in diverse postures that generate different (tensile or compressive) forces on it [Larson & Stern 1986, 1987, 1989; Roberts 1974]. The teres major is an important retractor of the humerus [Fleagle & Meldrum 1988; Larson & Stern 2007]. The relationship between the supraspinous and infraspinous fossae located on the dorsal side of the scapula is a commonly used parameter for determining the relationship between scapular morphology and locomotor patterns [Bello-Hellegouarch et al., 2013a; Frey 1923; Green et al., 2012; Inman et al., 1944; Roberts 1974; Schultz 1930].

General considerations

Among the external factors analyzed in this study that could potentially influence the scapular shape, locomotion was the factor that showed the highest correlations with the scapular shape (53.5%), followed by phylogeny at a family level (50.9%). Those correlations were consistent with the dispersion observed in the scatter plot. Although there was a clear clustering related to the evolutionary history of the species (each species generally being closer others from the same family), we could also observe the influence of the functional signal. For example, *Lagothrix*, instead of being closer to the other atelines *Ateles* and *Alouatta*, remained closer to other species with similar locomotor modes, such as the more strictly arboreal quadrupeds (i.e., *Colobus guereza*, *Cercopithecus mitis*, or *Cercopithecus ascanius*). Prosimians (Lemuridae, Lorisidae, Tarsiidae, Galagidae), rather than sharing a similar scapular shape and being clustered together in the plot, showed high dispersion consistent with their diverse locomotor modes. Cercopithecids showed a gradient in their distribution related to their degree of terrestrial or arboreal quadrupedalism. Some studies confirm our results, suggesting that the phylogenetic signal in the scapula is weaker than the functional one [Preuschoft et al., 2010; Young 2008]. Consequently, morphological variations of the postcranium [Collard et al., 2001; Lockwood 1999; Pilbeam 1996; Ward 1997] and the shoulder in primates [Ashton & Oxnard 1963; Preuschoft et al., 2010; Young 2008] seem to be mainly adaptive, related to their function during locomotion rather than taxon-specific, and hence are not primarily determined by ancestry. Based on this idea, recent studies have suggested that mechanical stresses strongly influence some morphological traits of the scapula, showing a highly adaptive nature to the different forces associated with various locomotor modes [Green et al., 2012; Preuschoft et al., 2010]. However, a thorough examination of the differences observed among the species and the influence of phylogeny compared with the influence of function was beyond the scope of our study. By extracting the mean shape configurations related to a particular locomotor mode, rather than analyzing the scapula of a particular taxon, we isolated aspects of the scapular morphology that reflect different locomotor adaptations. In taking this approach, we avoided erroneously assigning morphological features related to the evolutionary history of the taxon to functional adaptation.

The remaining external factors that were analyzed showed significantly lower correlations with scapular shape, compared with locomotion and phylogeny. Accurately measuring a qualitative observation such as canopy level preference is extremely problematic, and thus the system employed to measure such factors may influence the results. The canopy level is directly related to the substrate size and shape, which presents different challenges that have morphological consequences [Fleagle 1999; Schmidt 2010; Terranova 1996; Turley et al., 2011]. Thus, it would be worthwhile to develop more accurate systems to measure the canopy-level preference (and the substrate preference) and to evaluate the effects of this factor on the scapular shape. Furthermore, body mass explained very little in relation to the scapular shape, contradicting the general assumption that body mass differences strongly influence skeletal morphology [Cant 1992; Schmidt 2010].

Morphology and function

Terrestrial quadrupeds' use of more extended, adducted limb postures limits anterior–posterior motion in the shoulder joint in the parasagittal plane [Fleagle 1999; Roberts 1974]. The body weight acts compressively across the glenohumeral joint during the support phase, insuring its integrity [Jouffroy et al., 1990; Roberts & Davidson 1975; Whitehead & Larson 1994]. *Arboreal quadrupeds*, unlike terrestrial ones, move through a three-dimensional discontinuous milieu, which requires a more mobile shoulder to use their forelimb into abducted positions [Fleagle 1999; Roberts & Davidson 1975]. Thus, rotator cuff muscles and their fossae, especially the supraspinatus, are assumed to be better developed in arboreal quadrupeds than in terrestrial ones [Larson & Stern 1987, 1989, 1992; Manaster 1979; Roberts 1974; Roberts & Davidson 1975]. Our results are not consistent with this assumption, since terrestrial quadrupeds (Fig. 4c) appear to share a broader supraspinous fossa in relation to the arboreal quadrupeds (Fig. 4a), as well as a long scapular spine. This finding might be related to the need for stabilization of the glenohumeral joint to withstand the compressive forces resulting from a ground reaction to weight bearing during the support phase of the terrestrial quadrupedal locomotion [Kimes et al., 1981; Larson & Stern 1989, 1992; Oxnard 1967, 1976; Potau et al., 2011; Preschoft et al., 2010; Whitehead & Larson 1994]. The scapula related to *semiterrestrial quadrupedalism* (Fig. 4b) appears to be an intermediate shape between the scapulae associated with terrestrial and arboreal quadrupedalism, which is consistent with previous studies [Anapol & Gray 2003]. The teres major helps in retracting the humerus to lift the hand off the substrate and in the support/swing transition [Larson & Stern 1989, 2007; Whitehead & Larson 1994]. However, differences are very subtle, remaining the shape of all quadrupeds quite similar. Differences among terrestrial, semiterrestrial, and arboreal quadrupedal primates seem to be significantly higher in the arm muscles, rather than the shoulder muscles [Anapol & Gray 2003].

During the *bimanual suspension* performed by *Ateles* and to a lesser extent by *Lagothrix*, the forelimbs are completely extended overhead. In order to enhance their reach in all directions, the scapula is relatively short and wide (Fig. 4d) and positioned dorsally on the rib cage rather than laterally. These characteristics create a large difference compared with the rest of pronograde primates, whose scapulae are located in the parasagittal plane [Fleagle 1999; Larson 1993]. Thus, suspensory atelines, and especially *Ateles*, have converged on an ape-like postcranial anatomy [Andrews & Grove 1976; Corrucini & Ciochon 1978; Erikson 1963; Larson 1998] due to these suspensory behaviors. However, those suspensory platyrrhines differ from hominoids mainly by their prehensile tail acting as a fifth limb during the support phase of their bimanual progression [Carpenter & Durham 1969; Mittermeier 1978; Mittermeier & Fleagle 1976]. Their glenohumeral joint must be highly mobile to allow the free movements of the forelimbs to reach the branches situated overhead. Thus, those animals require a well-developed infraspinatus, the principal muscle that stabilizes the glenohumeral joint against transarticular tensile stresses during pendant suspension and the support phase of arm-swinging [Larson 1995; Larson & Stern

1986; Roberts 1974]. The supraspinous fossa is broad, but not as expected in a suspensory primate that performs anti-pronograde activities with the forelimbs in abducted and elevated positions [Cant 1986; Larson & Stern 1986, 1987]. Arm abduction in suspensory platyrrhines is mainly provided by the deltoid muscle, and development of an extremely hypertrophied supraspinatus muscle is unnecessary to protract the arm [Youlatos 2000].

Quadrupedal suspension (Fig. 4e), which is typical for arboreal primates such as lorisids and *Ateles*, is characterized by a horizontal movement below the substrate in an inverted (dorsal-side down) position using all four limbs in tension [Fujiwara et al., 2011; Hunt et al., 1996; Napier 1967]. Thus, the requirements of the shoulder muscles are similar to those present during the bimanual suspension; that is, relatively broad infraspinatus muscle are needed to stabilize the glenohumeral joint against transarticular tensile stresses during pendant suspension [Larson 1995; Larson & Stern 1986; Roberts 1974] and a relatively well-developed supraspinatus muscle is needed to abduct and elevate the upper limb [Larson & Stern 1986, 1987]. The slightly reduced fossae compared with the bimanual suspensory primates can be explained by the participation of the hindlimbs in the progression of the movement.

Pronograde clambering differs from quadrupedalism in its lack of a consistent gait pattern and requires a more pronounced limb abduction [Lockwood 1999; Youlatos 2000]. Their related scapular morphological features (Fig. 4f) appear to be similar to the adaptations to bimanual suspension, with slightly shorter infraspinous and teres major fossae and a remarkably broader supraspinous fossa. This broad supraspinous fossa can be related to need for abduction and forelimb elevation [Youlatos 2000].

Slow-climbing quadrupedalism consists of a smooth, slow, and deliberate form of quadrupedal locomotion than involves diagonal couplets in lateral sequence gait [Demes et al., 1990; Ishida et al., 1992; Jouffroy & Petter 1990]. During the support phase, which is much longer than the swing phase, the shoulder joint is abducted and laterally rotated to the extent that the trunk is close to the pole [Ishida et al., 1992]. This position requires a relatively well-developed infraspinatus muscle, and thus a broad infraspinous fossa [Gebo 1989; Roberts 1974; Roberts & Davidson 1975]. The infraspinatus muscle acts as the primary synergist to the deltoid in motions combining lateral rotation with arm abduction, such as overhead reaches and climbing [Larson & Stern 1986]. Moreover, the species that perform this locomotor behavior, such as lorisines (*Nycticebus coucang* and *Perodicticus potto* in our study), move through a three-dimensional support environment, which requires a mobile glenohumeral joint to reach the branches found at different levels, and stabilization of the joint must be maintained by relatively well-developed supraspinatus and infraspinatus muscles (Fig. 4g) [Gebo 1989; Higurashi et al., 2007; Larson & Stern 1986, 1989, 1992; Oxnard 1967; Roberts & Davidson 1975].

Less evident are the adaptations associated with the locomotor mode known as *leaping* (Fig. 4h), since the majority of the extreme adaptations to this form of locomotion are found in the hindlimb [Demes et al., 1996; Runestad Connour et al., 2000]. The leap is primarily powered by the hindlimb, and many leapers tend to land on their hindlimbs as well, while some of the larger species often land forelimb first [Demes et al., 1996]. Forelimbs of large-bodied leapers, such as *Lemur* or *Eulemur*, are particularly important in body positioning during the acceleration for takeoff and during the aerial phase of the leap when they raise their forelimbs above the head to increase the moment of inertia of the upper body [Demes et al., 1996; Dunbar 1988; Terranova 1996]. Thus, their glenohumeral joint require some mobility to use their forelimbs for kinematic purposes, hence the relatively well-developed supraspinous fossa, and an infraspinous fossa that is broader than that found in the specialized small-bodied *vertical-clingers* and *leapers*, which use their tails instead of their forelimbs for body position adjustments [Demes et al., 1996].

During *vertical-clinging* and *leaping*, forelimbs are not directly utilized during traveling; therefore, the primates don't need strong rotator cuff muscles because the forelimbs are more suitable for controlling more rapid locomotor movements with greater precision [Higurashi et al., 2007; Roberts & Davidson 1975]. Scapulae are reduced, long, and narrow (Fig. 4i), and although the shoulder joint is capable of raised-arm movements, the capability for adduction and abduction is reduced [Gebo 1989; Roberts 1974; Roberts & Davidson 1975]. In consequence, the primates have relatively reduced supraspinous, infraspinous, and teres major fossae. More adaptations for leaping must be found in the hindlimb, rather than the forelimb [Demes et al., 1996; Runestad Connour et al., 2000].

Vertical-clinging is characterized by a lesser need for shoulder stability through activity of the rotator cuff muscles [Fleagle & Meldrum 1988]. Further, the need for a relatively well-developed teres major muscle, a major retractor (adductor) of the humerus relative to the scapula, is very important in climbing and clinging [Fleagle &

Meldrum 1988]. However, we observed great difference between the scapulae of vertical clingers (Callitrichidae and *Pithecia*) and those of vertical-clingers and leapers (*Tarsius* and *Galago*) with regard to the length of the fossae and the scapular spine. Compared with the vertical-clingers and leapers, vertical-clingers appear to need relatively more developed supraspinatus, infraspinatus, and teres major muscles (Fig. 4j), possibly due to their use of clinging as a mode of displacement, while VCL use clinging as a postural behavior and leap from this clinging position [Kinzey et al., 1975; Napier 1967; Napier & Walker 1967].

The scapular shapes are theoretical shapes, with the morphological adaptations related to a specific locomotor mode isolated for its better comprehension. Most species of primates use more than one locomotor mode to progress through their habitat [Fleagle 1999; Hunt et al., 1996]. Thus, the shape of their scapulae will be the result of a compromise between the different requirements of the different modes of locomotion performed. For instance, we found that the scapula of terrestrial quadrupeds is characterized by a relatively broader supraspinous fossa than the scapula of arboreal quadrupeds. However, many studies have revealed that terrestrial quadrupeds actually have a relatively smaller supraspinous fossa than arboreal ones, due to the projection of the greater tubercle of the humerus, which increases the leverage of the supraspinatus muscle [Larson & Stern 1987, 1989, 1992; Manaster 1979; Roberts 1974; Roberts & Davidson 1975]. Species that perform arboreal quadrupedalism do not do so exclusively, but rather they usually leap, cling, or perform other modes of locomotion, which require a relatively broader supraspinous fossa than would be expected in a "pure" arboreal quadruped. Further, we must take into account that there is no simple relationship between anatomy and behavior; that is, similar behaviors may be performed by using different morphological features, while similar anatomical features can fulfill the mechanical demands of more than one behavior [Bock & von Wahlert 1965; Fleagle 1999; Ruff & Runestad 1992; Ward & Sussman 1979].

We are aware that our classification of the locomotor modes of primates is not as accurate as we would desire. It is exceptionally problematical to precisely classify the actual locomotor modes because primates exhibit high versatility in locomotor behaviors. They combine behaviors in such an extreme way that not only do they vary among genus or subfamilies [Preuschoft 1989], but also among individuals and their environment. Therefore, we placed more emphasis on frequent locomotor behaviors of the different species of pronograde primates to simplify the categorization and the posterior analysis. However, many of these species are capable of infrequent, but still critical behaviors [Prost 1965] that are essential for food acquisition or for escape. These behaviors are characterized by high loadings on the bone, and they may affect the scapular shape in some way, despite their low frequency [Martin 1990; Schmidt 2010; Rose 1973]. Moreover, it has been suggested that forelimb positional functions that are unrelated to locomotion, such as reaching for food and grooming, would more heavily impact forelimb anatomy than locomotor adaptations [Hanna et al., 2006; Larson 1998; Larson et al., 2000; McGraw 1998; Stevens 2008; Wright-Fitzgerald et al., 2010]. Nevertheless, some authors have observed that the forces transmitted across the shoulder during postural behaviors are smaller than those in locomotion and do not require any special adaptations

[Preuschoft et al., 2010; Roberts 1974; Rose 1974]. Further, Anapol & Gray [2003] suggested that these positional functions would be more likely to affect the morphology of the forearm and hand rather than the shoulder.

In summary, further analyses employing more precise and realistic locomotor categories are needed to understand more exactly the anatomical and morphological requirements of each particular locomotor mode observed in this taxon. Our results, however, can serve as a basis for more detailed analyses of the morphology of the scapula and its locomotor adaptations in primates.

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5. Expression of myosin heavy chain isoforms in the supraspinatus muscle of different primate species: implications for the study of the adaptation of primate shoulder muscles to different locomotor modes.

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RESUMEN

Este estudio cuantifica mediante *Real-Time PCR* (RT-PCR) la expresión de mRNA de las tres isoformas de la cadena pesada de la miosina (MHC) en el músculo supraespinoso de humanos modernos y 12 especies de primates con diferentes modos de locomoción, con el fin de caracterizar factores funcionales del músculo supraespinoso en relación con los modos de locomoción observados en los primates. Los resultados muestran una clara asociación entre la función del músculo supraespinoso, tanto en primates pronógrados como en ortógrados, con el patrón de expresión de las isoformas de MHC.

Ninguno de los primates pronógrados expresa la isoforma MHC-IIx en el músculo supraespinoso. Esta isoforma, la más rápida y menos resistente, no se expresa en músculos posturales lentos (Fitts *et al*. 1991; Baldwin 1996; Fitts & Schiaffino & Reggiani 1996; Rivero *et al*. 1999; Talmadge 2000). Los resultados obtenidos confirman a nivel molecular la importancia del músculo supraespinoso como músculo postural, estabilizador de la articulación, en primates pronógrados. En cambio, el músculo supraespinoso de los primates ortógrados (incluidos los humanos modernos) expresa las tres isoformas de MHC, con una mayor expresión de las dos isoformas más rápidas (MHC-II). Este patrón de expresión es típico de músculos rápidos y potentes pero con poca resistencia a la fatiga (Klitgaard *et al*. 1990; Harridge *et al*. 1996), que reforzarían la función elevadora del músculo supraespinoso en los primates ortógrados. Aunque los primates ortógrados no humanos emplean varios modos de locomoción (braquiación, *arm-swinging*, *knuckle-walking*),

no se encontraron diferencias significativas en los patrones de expresión de las isoformas de MHC en relación con sus modos de locomoción.

Los humanos modernos mostraron un patrón de expresión de MHC similar al de los primates ortógrados, aunque con una mayor porcentaje de expresión de la isoforma MHC-IIx y, por tanto, un menor porcentaje de la isoforma MHC-IIa. Esta mayor expresión de la isoforma más rápida favorecería la movilidad y precisión de los músculos de la extremidad anterior en humanos modernos, que tiene una función eminentemente manipulativa.

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Expression of Myosin Heavy Chain Isoforms in the Supraspinatus Muscle of Different Primate Species: Implications for the Study of the Adaptation of Primate Shoulder Muscles to Different Locomotor Modes

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Abstract The supraspinatus muscle is a key component of the soft tissues of the shoulder. In pronograde primates, its main function, in combination with the other rotator cuff muscles (subscapularis, infraspinatus, and teres minor), is to stabilize the glenohumeral joint, whereas in orthograde primates it functions together with the deltoid, to elevate the upper extremity in the scapular plane. To determine whether these functional differences are also reflected in the molecular biochemistry of the supraspinatus muscles involved in these different locomotor modes, we used real-time polymerase chain reaction (RT-PCR) to analyze the expression of the myosin heavy chain (MHC) isoforms in supraspinatus muscles from modern humans and 12 species of pronograde and orthograde primates. The MHC expression pattern in the supraspinatus muscle of pronograde primates was consistent with its function as a tonic and postural muscle, whereas the MHC expression pattern observed in the supraspinatus muscle of nonhuman orthograde primates was that of a muscle that emphasizes speed, strength, and less resistance to fatigue. These findings are

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consistent with the role of the supraspinatus in the posture and locomotor modes of these groups of nonhuman primates. The humans included in the study had an expression pattern similar to that of the nonhuman orthograde primates. In conclusion, molecular analysis of skeletal muscles via RT-PCR can contribute to a better understanding of the morphological and functional characteristics of the primate musculoskeletal system.

Keywords Myosin heavy chain · Primate locomotion · Real-time polymerase chain reaction · Supraspinatus

Introduction

The supraspinatus muscle, together with the subscapularis, infraspinatus, and teres minor muscles, forms part of the rotator cuff, which plays an important role in the movement and stabilization of the glenohumeral joint (Ashton and Oxnard 1963; Michener *et al*. 2003; Roberts 1974). The anatomical and functional characteristics of the supraspinatus vary among the different species of primates according to their posture and locomotor mode. Pronograde primates are characterized by a narrow thorax, a scapula located in the parasagittal plane, and a glenohumeral joint adapted for both arboreal and terrestrial quadrupedal locomotion. Orthograde primates, which include the family Hylobatidae (gibbons) and the species *Pongo pygmaeus* (orangutans), *Gorilla gorilla* (gorillas), *Pan troglodytes* (chimpanzees), *Pan paniscus* (bonobos), and *Homo sapiens* (modern humans), are characterized by a broad thorax, a more dorsally situated scapula, and a more mobile glenohumeral joint suitable for different locomotor modes—including brachiation, vertical climbing, suspensory posture and knuckle-walking—and in modern humans consistent with using the hand for complex manipulation (Aiello and Dean 1990; Schultz 1961).

In pronograde primates such as *Chlorocebus aethiops* (Larson and Stern 1989), *Papio anubis*, and *Macaca mulatta* (Larson and Stern 1992), the supraspinatus muscle is electromyographically active during the support phase of quadrupedal walking, acting as a stabilizer of the glenohumeral joint. Nonprimate quadrupeds, such as *Felis catus* (cat: English 1978) and *Didelphis virginiana* (Virginia opossum: Jenkins and Weijs 1979), have a similar pattern of activity. This function of stabilizing the glenohumeral joint is also important in orthograde primates using quadrupedal locomotion, such as gorillas and chimpanzees. Investigators have also recorded electromyographic activity in the supraspinatus in these primates during the support phase of knuckle-walking (Larson and Stern 1987; Tuttle and Basmajian 1978).

In addition to stabilizing the glenohumeral joint, the supraspinatus muscle works together with the deltoid muscle to elevate the upper extremity in the scapular plane (Alpert *et al*. 2000; Basmajian and de Luca 1985; Halder *et al.* 2001; Inman *et al.* 1944). This function is especially important in orthograde primates, in which the anatomical structure of the thorax and the shoulder allows the upper extremity to be elevated during brachiation, vertical climbing, and suspensory locomotion (Ashton and Oxnard 1964; Ciochon and Corruccini 1977; Inman *et al.* 1944; Oxnard 1963, 1967). The supraspinatus muscle of orthograde primates such as orangutans, gorillas, chimpanzees, and modern humans also shows electromyographic activity during the elevation of the hand (Inman *et al.* 1944; Larson and Stern 1986; Tuttle and Basmajian 1978).

The morphology of the supraspinatus muscle is adapted to the type of locomotion used by each species of primates. For example, the size, i.e., mass, of the supraspinatus relative to the total mass of deltoid, rotator cuff, and teres major muscles was larger in pronogrades than in hominoids (Inman *et al.* 1944). In addition, the difference in size between the supraspinatus fossa and the infraspinatus fossa is much greater in arboreal quadrupedal primates (*Miopithecus talapoin* and *Colobus* sp.) than in terrestrial or semiterrestrial quadrupedal primates (*Papio papio*, *Macaca* sp., *Chlorocebus aethiops*, and *Erythrocebus patas*: Roberts 1974). Similarly, the supraspinatus fossa is larger in relation to the infraspinatus fossa in orangutans than in arboreal quadrupedal primates, and it is larger still in chimpanzees and gorillas, both knuckle-walkers (Roberts 1974). Modern humans seem to be the exception among orthograde primates because their supraspinatus fossa is relatively small (Roberts 1974). The smaller supraspinatus fossa in terrestrial quadrupedal primates may be due to the shape of the humeral head, which is less spherical in terrestrial than in arboreal quadrupedal primates, with a resultant greater projection of the greater tubercle and greater leverage for the supraspinatus (Larson 1993). Different locomotor modes also lead to differences in the internal structure of the supraspinatus, e.g., angle of pinnation and muscle fiber length. In *Chlorocebus aethiops*, semiterrestrial quadrupeds, the internal structure of the supraspinatus is adapted for speed instead of strength, vs. *Cercopithecus ascanius*, arboreal quadrupeds, in which strength is a more important factor (Anapol and Gray 2003). In modern humans, the internal structure of the supraspinatus is designed for great strength but in small movements (Ward *et al.* 2006).

The skeletal muscles of adult mammals express 3 MHC isoforms—the slow MHC-I, the fast MHC-IIa, and the fastest MHC-IIx—in different proportions. A fourth isoform, MHC-IIb, is expressed only in skeletal muscles of very small mammals (Baldwin and Haddad 2001). The expression pattern of the MHC isoforms is directly related to the functional properties of the muscle fibers (Table I), such as contraction time, strength, and resistance to fatigue (Bottinelli and Reggiani 2000). The MHC-I isoform is expressed mainly in slow-oxidative, or type I, fibers; the MHC-IIa isoform in fast-oxidative, glycolytic, or type IIa, fibers; and the MHC-IIx isoform in fast glycolytic, or type IIx fibers. Type IIx fibers are more powerful, faster, and less resistant to fatigue than type IIa fibers, while type I fibers are the least powerful and fast, but the most fatigue-resistant of the 3 types (Botinelli *et al.* 1999; Pette and Staron 2000). In general, the slow postural muscles express mainly the slow MHC-I isoform, with a variable expression of the MHC-IIa isoform (Baldwin 1996; Fitts and Widrick 1996; Fitts *et al.* 1991; Rivero *et al.* 1999; Schiaffino and Reggiani 1996; Talmadge 2000). In contrast, the powerful, fast, but less fatigue-resistant muscles express all 3 MHC isoforms in variable proportions but with a generally higher expression of the MHC-II isoforms (Harridge *et al.* 1998; Larsson and Moss 1993).

Using ATPase staining, Singh *et al.* (2002) found that the supraspinatus of *Macaca mulatta* had a mean of 49% of type I fibers, 23% of type IIa fibers, and

Table I Main characteristics of the muscle fiber types of mammalian muscles

	Type I fibers	Type IIa fibers	Type IIx fibers
MHC isoform predominantly expressed	MHC-I	MHC-Iia	MHC-IIx
Metabolism	Slow oxidative	Fast oxidative	Fast glycolytic
Contraction velocity	Slow	Fast	Very fast
Resistance to fatigue	High	Intermediate	Low
Force production	Low	High	Very high
Mitochondrial density	High	High	Low
Oxidative capacity	High	High	Low
Glycolytic capacity	Low	High	High
Myoglobin content	High	High	Low
Capillary density	High	High	Low
Identification method	ATPase staining	ATPase staining	ATPase staining

MHC = myosin heavy chain

28% of type IIx fibers. Using the same technique, Schmidt and Schilling (2007) found that the percentage of type I fibers in the supraspinatus of *Saguinus oedipus* was greater than in the supraspinatus of *Saimiri sciureus* (55–70% vs. 45–60%, respectively), which the authors attributed to the greater stability of the glenohumeral joint in *Saguinus oedipus* and its greater mobility in *S. sciureus*. These authors also reported a heterogeneous distribution of the fiber types; the percentage of type I fibers increased from proximal to distal, and in the more proximal region, type I fibers were concentrated in the posterior muscle region near the scapular spine (Schmidt and Schilling 2007). Also using ATPase staining, Srinivasan *et al.* (2007) found that the supraspinatus of *Homo sapiens* had a mean of 50% of type I fibers, 21% of type IIa fibers, and 29% of type IIx fibers. Using immunohistochemistry with antibodies for specific MHC isoforms, Lovering and Russ (2008) found that the MHC-I isoform accounted for 54% of MHC expression in the modern human supraspinatus.

Although there is abundant information in the literature about the anatomy and the structure of the supraspinatus in different primate species, to date few studies have examined the molecular characteristics of this muscle, and the majority of them have been conducted in a small number of species. Most studies have analyzed the quantification and distribution of the different fiber types in the skeletal muscle (Schmidt and Schilling 2007; Singh *et al.* 2002), but none have examined the mRNA expression of the different MHC isoforms in the supraspinatus. Real-time quantitative polymerase chain reaction (RT-PCR) analysis of the MHC isoforms can provide new information on the molecular characteristics of the supraspinatus muscle in different primate species and their relation to different types of locomotion. RT-PCR has several advantages over both ATPase staining and immunohistochemistry. ATPase staining can be used only with muscles obtained from biopsies or immediately after death, because results can vary due to postmortem changes in pH. However, RT-PCR can be used with muscles from cryopreserved cadavers because any potential postmortem degradation of the mRNA can be accounted for by normalizing the values of each MHC isoform with those of the endogenous gene 18 S, which remains intact for ≥8 d postmortem in the skeletal muscle (Bahar *et al.* 2007). Whereas immunohistochemistry does not distinguish between the MHC-IIa and the MHC-IIx isoforms, RT-PCR can identify all 3 MHC isoforms.

In the present study, we quantified the mRNA expression of the 3 MHC isoforms by RT-PCR in supraspinatus muscles from modern humans and 12 different species of primates. Our primary objective was to obtain molecular information on the functional characteristics of the supraspinatus muscle and to correlate our findings with adaptations of the supraspinatus to different locomotor modes. We hypothesized that a differential expression pattern of MHC isoforms would be related to the different functions of the supraspinatus in pronograde and orthograde primates.

Materials and Methods

Supraspinatus Muscle Samples

We obtained supraspinatus muscle samples from modern humans and nonhuman primates, cryopreserved within 24–48 h of death and not treated with any fixation method. The 24 modern human supraspinatus muscle samples included in the study were from cadavers from the Body Donation Service and dissection rooms of the University of Barcelona. The 12 male and 12 female cadavers, with a mean age of 74.8 yr (range, 44–97 yr), showed no macroscopic pathology. The 21 nonhuman primate supraspinatus muscle samples were obtained from 12 different species (Table II) from the Department of Anatomy and Radiology of the University of

Table II Means and standard deviations (SD) of the relative mass and mRNA expression of MHC isoforms in the supraspinatus muscle

Species	Sample	Locomotion	SUP/RC	% MHC-I	% MHC-II	% MHC-IIa	% MHC-IIx
Homo sapiens	24	B	0.16 (0.02)	36.86 (2.52)	63.14 (2.52)	33.38 (1.57)	29.77 (2.43)
Pan troglodytes	3	KW-AS	0.15 (0.01)	33.03 (2.07)	66.97 (2.07)	38.30 (2.42)	28.67 (1.98)
Gorilla gorilla	3	KW	0.20 (0.02)	36.77 (1.37)	63.23 (1.37)	35.69 (1.42)	27.54 (2.07)
Pongo pygmaeus	2	AS	0.18 (0.01)	37.64 (3.36)	62.36 (3.36)	39.43 (0.55)	22.94 (2.81)
Nomascus gabriellae	1	BR	0.17	33.59	66.41	35.79	30.62
Miopithecus talapoin	1	AQ	0.29	48.27	51.73	51.73	0
Macaca fascicularis	3	AQ	0.22 (0.01)	46.29 (4.01)	53.71 (4.01)	53.71 (4.01)	0
Colobus guereza	1	AQ	0.21	48.46	51.54	51.54	0
Lemur catta	2	STQ	0.25 (0.03)	53.46 (1.19)	46.54 (1.19)	46.54 (1.19)	0
Chlorocebus aethiops	1	STQ	0.26	49.51	50.49	50.49	0
Macaca silenus	2	STQ	0.26 (0.00)	48.15 (0.64)	51.85 (0.64)	51.85 (0.64)	0
Mandrillus sphinx	1	STQ	0.25	48.49	51.51	51.51	0
Erythrocebus patas	1	TQ	0.28	49.14	50.86	50.86	0

SUP = supraspinatus mass; RC = rotator cuff mass; B = biped; KW = knuckle-walker; AS = arm-swinger; BR = brachiator; AQ = arboreal quadruped; STQ = semiterrestrial quadruped; TQ = terrestrial quadruped

Valladolid. All of the focal subjects came from Spanish zoos and had died from causes unrelated to the present study. We included 9 orthograde primates: 1 male *Nomascus gabriellae* (gibbon), 2 female *Pongo pygmaeus*, 1 male and 2 female *Gorilla gorilla*, and 2 male and 1 female *Pan troglodytes*. We also included 12 pronograde primates: 2 female *Lemur catta*, 1 male *Miopithecus talapoin*, 1 male *Erythrocebus patas*, 1 female *Chlorocebus aethiops*, 2 male *Macaca silenus*, 3 male *Macaca fascicularis*, 1 male *Mandrillus sphinx*, and 1 female *Colobus guereza*. All the primates were adults, except the *Nomascus gabriellae*, which was 13 mo old.

In each specimen, the same investigator carefully dissected the subscapularis, supraspinatus, infraspinatus, and teres minor muscles (Figs. 1 and 2). He removed adipose tissue and fascia and recorded the weight of each of the muscles. He weighed each muscle 3 times at 5-min intervals and took the mean of the 3 measurements as the muscle's weight. He obtained the total weight of the rotator cuff (RC) for each individual by adding the weight of each of the muscles, and calculated the weight of the supraspinatus muscle (SUP) relative to the total RC (SUP/RC). Although the weight of the supraspinatus relative to total body weight may be a more appropriate parameter, we did not know the total body weight of the primates dissected because they were necropsied before our study was performed. We therefore selected the SUP/RC as a useful parameter to provide information on the degree of development of the supraspinatus in relation to the other stabilizers of the glenohumeral joint. After weighing the muscles, the investigator took 3 samples of 3–5 mm^3 from the central area of each of the supraspinatus muscles and froze them in saline solution for the molecular analyses.

In addition, to determine if MHC expression in the supraspinatus muscle is homogeneous or heterogeneous, we analyzed this expression in several regions of the supraspinatus of an orthograde primate (*Gorilla gorilla*) and a pronograde primate (*Macaca fascicularis*). We obtained samples from the anterior proximal, anterior central, anterior distal, posterior proximal, posterior central, and posterior distal regions of the supraspinatus. The proximal region of the supraspinatus corresponds to the region near the medial border of the scapula; the distal region is near the glenoid fossa; the anterior region is near the superior angle of the scapula;

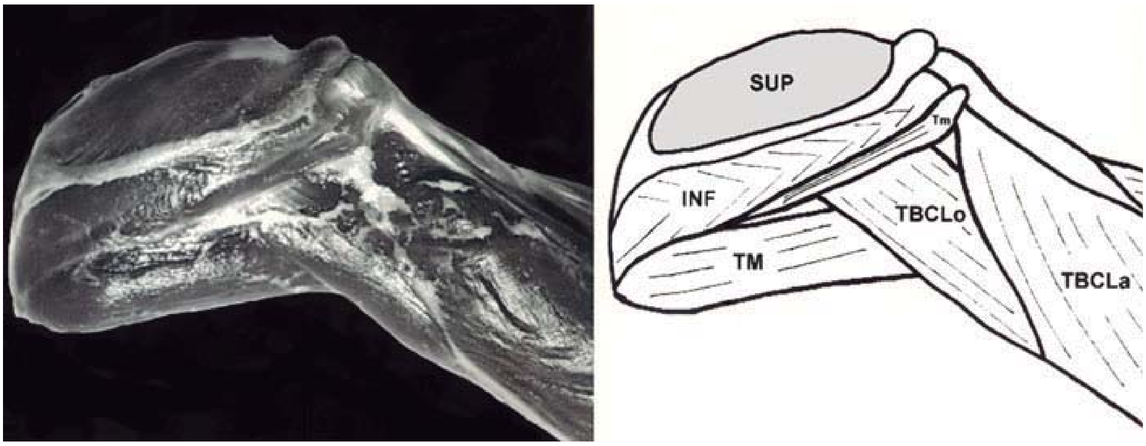

Fig. 1 Dissection and anatomical drawing of the dorsal region of the scapula in a pronograde primate (*Lemur catta*), showing the 3 posterior muscles of the rotator cuff and the teres major muscle. SUP = supraspinatus; INF = infraspinatus; Tm = teres minor; TM = teres major; TBCLo = triceps brachii caput longum; TBCLa = triceps brachii caput laterale.

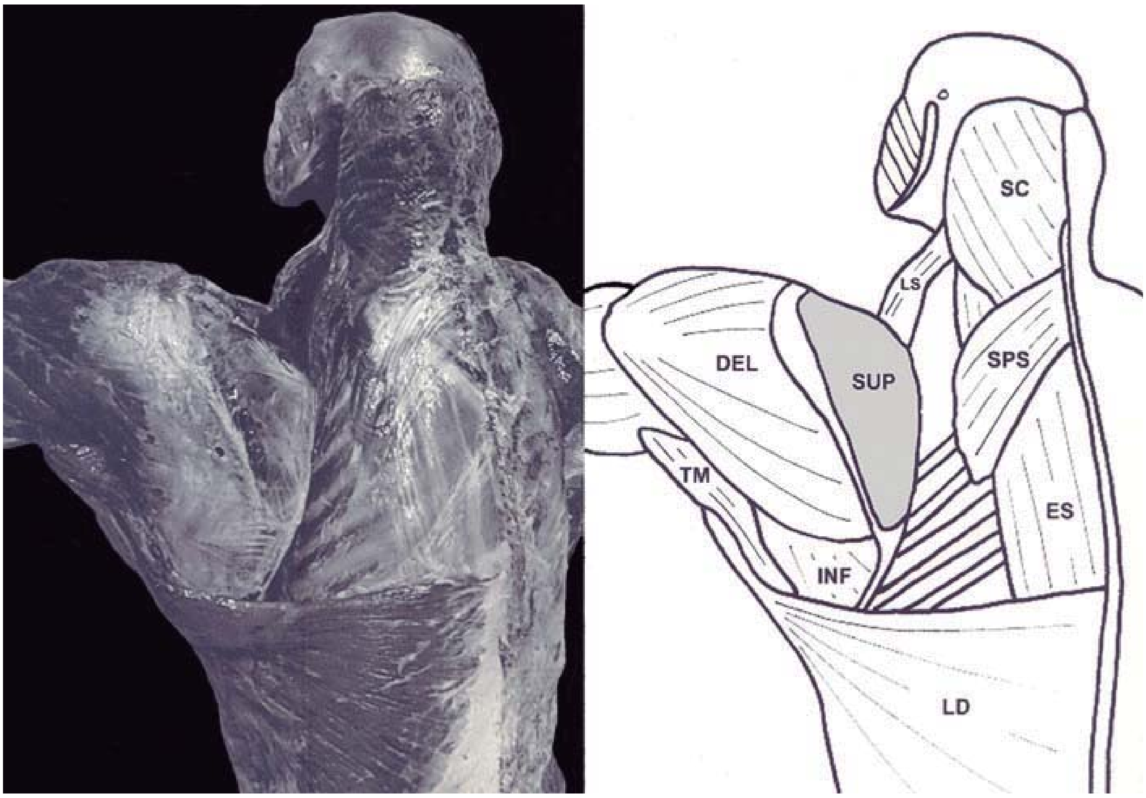

Fig. 2 Dissection and anatomical drawing of the dorsal region of the shoulder in an orthograde primate (*Pan troglodytes*) after the elimination of the trapezius, rhomboideus minor, and rhomboideus major muscles. SUP = supraspinatus; INF = infraspinatus; TM = teres major; DEL = deltoid; LD = latissimus dorsi; LS = levator scapulae; SC = splenius capitis; SPS = serratus posterior superior; ES = erector spinae.

the posterior region is near the scapular spine; and the central region is located between the proximal and the distal regions.

RNA Isolation and cDNA Synthesis

We extracted the RNA from the muscle samples using the commercial RNeasy mini kit (Qiagen, Valencia, CA) according to the manufacturer's protocol. We used UV spectrophotometry to determine the concentration, purity, and amount of RNA and electrophoresis on 1% agarose gels to assess the integrity and quality of RNA. We used a NanoDrop 1000 Spectrophotometer to quantify RNA from the samples in duplicate.

We used the TaqMan Reverse Transcription Reagent Kit (Applied Biosystems, Foster City, CA) to synthesize cDNA. We performed reverse transcription using 330 ng of total RNA in 10 μl of TaqMan RT buffer, 22 ml of 25 mM magnesium chloride, 20 μl of dNTPs, 5 μl of random hexamers, 2 μl of RNAse inhibitor, 2.5 μl of MultiScribe Reverse Transcription, and RNA sample plus RNAse-free water, for a final volume of 100 μl, in the following thermal cycler conditions: 10 min at 25°C, 48 min at 30°C, and 5 min at 95°C.

Gene Expression and Quantification by RT-PCR

Applied Biosystems supplied primers and probes. We labeled primers at the 5′ end with the reporter dye molecule FAM. We analyzed MYH-I (Hs00165276_m1), MYH-IIa (Hs00430042_m1), MYH-IIx (Hs00428600_m1), and MYH-IIb (Hs00757977_m1) genes. We used an 18 S gene probe labeled at the 5′ end with the reporter dye molecule FAM (Hs99999901_s1) as a housekeeping gene.

We performed RT-PCR in a total volume of 20 μl in the ABI Prism 7700 Sequence Detection System (Applied Biosystems). We ran all samples for each gene in duplicate for 40 cycles using the following master mix and thermal cycler conditions: 10 μl of the TaqMan universal PCR master mix, 1 μl of the primers and probes, 2 μl of the cDNA, and 7 μl of the RNAse-free water for 2 min at 50°C, 10 min at 95°C, 15 s at 95°C, and 1 min at 60°C. We used genomic DNA as negative control in each run. We captured fluorescent emission data and quantified mRNA concentrations by using the critical threshold value and $2^{-\Delta\Delta Ct}$.

Finally, we calculated the expression of each MHC isoform (MHC-I, MHC-IIa, and MHC-IIx) relative to the total expression of all MHC isoforms and compared the expression of the 2 fast MHC-II isoforms taken together to the expression of the slow MHC-I isoform.

Statistical Analyses

We divided the modern humans and nonhuman primates into ≥1 of 7 subgroups (Table II) based on their most commonly used substrate and locomotor mode, according to Schmitt (2010). The bipeds included *Homo sapiens*; the knuckle-walkers included *Pan troglodytes* and *Gorilla gorilla*; the arm-swingers included *Pan troglodytes* and *Pongo pygmaeus*; the arboreal quadrupeds included *Miopithecus talapion*, *Macaca fascicularis*, and *Colobus guereza*; the semiterrestrial quadrupeds included *Lemur catta*, *Chlorocebus aethiops*, *Macaca silenus*, and *Mandrillus sphinx*; the brachiators included *Nomascus gabriellae*; and the terrestrial quadrupeds included *Erythrocebus patas*.

We used the Mann-Whitney test to compare orthograde vs. pronograde taxa and to compare the locomotor groups that contained ≥5 individuals each: bipeds (24 individuals), knuckle-walkers (6 individuals), arm-swingers (5 individuals), arboreal quadrupeds (5 individuals), and semiterrestrial quadrupeds (6 individuals). We set statistical significance at $p<0.05$. We used SPSS version 14.0 for all statistical analyses.

Results

Table II summarizes the results. The mean SUP/RC values are 0.16 in modern humans, 0.18 in nonhuman orthograde primates, and 0.25 in pronograde primates. We observed significant differences between modern humans and nonhuman orthograde primates ($p=0.018$, $U=49.5$, df=31), between modern humans and pronograde primates ($p<0.001$, $U=0$, df=34), and between nonhuman orthograde and pronograde primates ($p<0.001$, $U=5$, df=19). In the subgroups based on locomotor mode, the mean SUP/RC values are as follows: bipeds, 0.16; knuckle-walkers, 0.18; arm-swingers, 0.16; arboreal quadrupeds, 0.23; and semiterrestrial quadrupeds, 0.25. We observed significant differences in SUP/RC values between bipeds and arboreal quadrupeds ($p=0.001$, $U=0$, df=27), between bipeds and semiterrestrial quadrupeds ($p<0.001$, $U=0$, df=28), between knuckle-walkers and arboreal quadrupeds ($p=0.045$, $U=4$, df=9), between knuckle-walkers and semiterrestrial quadrupeds ($p=0.006$, $U=1$, df=10), between arm-swingers and arboreal quadrupeds ($p=0.009$, $U=0$, df=8), and between arm-swingers and semiterrestrial quadrupeds ($p=0.006$, $U=0$, df=9). We observed no significant differences between bipeds and knuckle-walkers ($p=0.092$, $U=39.5$, df=28), between bipeds and arm-swingers ($p=0.371$, $U=44.5$, df=27), or between arboreal quadrupeds and semiterrestrial quadrupeds ($p=0.144$, $U=7$, df=9).

The expression pattern of the MHC isoforms is similar in the modern humans and the nonhuman orthograde primates, with higher expression levels of the MHC-II isoforms. The mean expression of the MHC-I isoform is 36.86% in modern humans and 35.36% in nonhuman orthograde primates ($p=0.157$, $U=73$, df=31). The mean expression of the 2 MHC-II isoforms taken together is 63.14% in modern humans and 64.64% in nonhuman orthograde primates ($p=0.157$, $U=73$, df=31). However, modern humans expressed a higher proportion of the MHC-IIx isoform (29.77% vs. 27.24%; $p=0.043$, $U=58$, df=31) and a lower proportion of the MHC-IIa isoform (33.38% vs. 37.4%; $p<0.001$, $U=10$, df=31). The pronograde primates have a higher proportion of the MHC-I isoform (48.83%) and a lower proportion of the MHC-II isoforms (51.17%) than either the modern humans ($p<0.001$, $U=0$, df=34) or the nonhuman orthograde primates ($p<0.001$, $U=0$, df=19). Intriguingly, none of the pronograde primates expressed MHC-IIx, though all the modern human and nonhuman orthograde primates expressed it. None of the modern humans or nonhuman primates expressed MHC-IIb.

The overall pattern of MHC expression is similar in the biped, knuckle-walker, and arm-swinger subgroups. There are no significant differences in the expression of MHC-I between bipeds and knuckle-walkers ($p=0.120$, $U=42$, df=28) or between bipeds and arm-swingers ($p=0.133$, $U=34$, df=27). There are no significant differences in the expression of MHC-IIx between bipeds and knuckle-walkers ($p=0.133$, $U=43$, df=28) or between bipeds and arm-swingers ($p=0.050$, $U=26$, df=27). However, the bipeds have a lower expression of MHC-IIa (33.38%) than the knuckle-walkers (36.99%) ($p=0.001$, $U=10$, df=28) and the arm-swingers (38.75%; $p=0.001$, $U=0$, df=27). In contrast, we observed significant differences in the expression of all 3 MHC isoforms when we compared the biped, knuckle-walker, and arm-swinger subgroups to the arboreal quadruped and the semiterrestrial quadruped subgroups. In the arboreal quadruped subgroup, the mean expression is 47.12% of MHC-I and 52.88% of MHC-IIa (arboreal quadrupeds vs. bipeds, $p=0.001$, $U=0$, df=27; arboreal quadrupeds vs. knuckle-walkers, $p=0.006$, U=0, df=7; arboreal quadrupeds vs. arm-swingers, $p=0.009$, $U=0$, df=8). In the semiterrestrial quadruped subgroup, the mean expression is 50.20% of MHC-I and 49.8% of MHC-IIa (semiterrestrial quadrupeds vs. bipeds, $p<0.001$, $U=0$, df=28; semiterrestrial quadrupeds vs. knuckle-walkers, $p=0.004$, $U=0$, df=10; semiterrestrial quadrupeds vs arm-swingers, $p=0.006$, $U=0$, df=7). We observed no significant differences in MHC isoform expression between the arboreal quadruped and the semiterrestrial quadruped subgroups ($p=0.100$, $U=6$, df=7).

There are no large variations in the MHC expression pattern according to the region of the supraspinatus muscle studied in 1 *Macaca fascicularis* and 1 *Gorilla gorilla* (Table III).

Table III mRNA expression of MHC isoforms in different regions of the supraspinatus muscle in 1 *Macaca fascicularis* and 1 *Gorilla gorilla*

Species	Region analyzed	% MHC-I	% MHC-IIa	% MHC-IIx
Macaca fascicularis	Anterior	46.8	53.2	0
	Posterior	46.32	53.68	0
	Proximal	46.64	53.36	0
	Central	46.77	53.23	0
	Distal	46.27	53.73	0
Gorilla gorilla	Anterior	33.43	36.15	30.42
	Posterior	34.17	36.13	29.7
	Proximal	34.26	36.2	29.54
	Central	34.23	36.12	29.65
	Distal	32.91	36.1	30.99

Discussion

In the present study, the mass of the supraspinatus muscle in relation to the total mass of the rotator cuff was larger in the pronograde than in modern humans and the nonhuman orthograde primates. These findings are in line with those of Inman *et al.* (1944), who compared the mass of the supraspinatus muscle with the combined mass of all the scapulohumeral muscles, including the rotator cuff, the deltoid, and the teres major muscles. The supraspinatus plays an important role in stabilizing the glenohumeral joint in the pronograde primates, preventing its collapse in retraction (Preuschoft *et al.* 2010). This role of the supraspinatus as an antigravity postural muscle may explain its larger proportional size in pronograde vs. orthograde primates because postural muscles, such as the human soleus or gluteus maximus, tend to be relatively large.

In contrast, in modern humans and nonhuman orthograde primates, the primary role of the supraspinatus muscle is the elevation of the upper extremity in the scapular plane, where it acts together with the deltoid (Inman *et al.* 1944; Larson and Stern 1986; Tuttle and Basmajian 1978). The relatively smaller size of the supraspinatus in modern humans and the nonhuman orthograde primates in comparison with the pronograde primates may be due to its role as an agonist of the deltoid muscle, which is especially large in hominoid primates (Aiello and Dean 1990; Inman *et al.* 1944). The different locomotor modes of modern humans and the nonhuman orthograde primates do not seem to be related to major changes in the relative size of the supraspinatus muscle because we found no significant differences in SUP/RC values among the biped, knuckle-walker, and arm-swinger subgroups. The SUP/RC values for the chimpanzees, orangutans, and the gibbon were similar to those for modern humans. However, the gorillas had a higher SUP/RC value. This proportionately larger supraspinatus may be related to the fact that the fundamental locomotor mode of adult gorillas is knuckle-walking (Fleagle 1999; Schmitt 2010), wherein the supraspinatus muscle is crucial to the stability of the glenohumeral joint (Larson and Stern 1987; Tuttle and Basmajian 1978). However, this larger supraspinatus was not evident in the chimpanzees, which combine knuckle-walking with other locomotor modes, including arm-swinging (Schmitt 2010). Further studies with a larger number of chimpanzees and gorillas could help shed light on the potential effect of knuckle-walking on SUP/RC values.

The functional differences between the supraspinatus muscles of modern humans and nonhuman orthograde primates and pronograde primates are reflected in the differences in MHC expression patterns. Importantly, none of the pronograde primates expressed MHC-IIx in the supraspinatus muscle. MHC-IIx is the fastest and least resistant of the MHC isoforms and is not expressed in slow postural muscles (Baldwin 1996; Fitts and Widrick 1996; Fitts *et al.* 1991; Rivero *et al.* 1999; Schiaffino and Reggiani 1996; Talmadge 2000). Our findings thus provide molecular evidence for the importance of the supraspinatus as a postural muscle in pronograde primates. In relation to MHC-I isoform expression, our results confirm previous findings with ATPase staining in other pronograde primates, such as *Macaca mulatta* (Singh *et al.* 2002) and *Saimiri sciureus* (Schmidt and Schilling 2007). Specifically, Singh *et al.* (2002) found 44–58% of type I fibers in the supraspinatus muscle of *Macaca mulatta*, and Schmidt and Schilling (2007) found 45–60% of type I fibers in the supraspinatus of *Saimiri sciureus*. These percentages are along the lines of the 42.48–54.30% of MHC-I expression we observed in the 12 pronograde primates in the present study.

Schmidt and Schilling (2007) observed a heterogeneous distribution of the type I fibers in the supraspinatus of *Saguinus oedipus* and *Saimiri sciureus*, with a major percentage of these fibers in the distal region of the muscle and near the scapular spine. Intriguingly, however, we have observed a homogeneous expression of the MHC isoforms in the supraspinatus muscle of both *Macaca fascicularis* and *Gorilla gorilla*, leading us to speculate that the distribution of fiber types may be unrelated to the expression of MHC isoforms. Further analyses with a wider sample of primate species and individuals are warranted to shed light on this issue.

In contrast to that of the pronograde primates, the supraspinatus of all the modern humans and nonhuman orthograde primates expressed all 3 MHC isoforms, with a higher percentage of the 2 fast MHC-II isoforms than the slow MHC-I isoform. This expression pattern is typical of fast and powerful muscles with low resistance to fatigue (Harridge *et al.* 1996; Klitgaard *et al.* 1990), and our findings provide evidence for the elevatory function of the supraspinatus in pronograde primates. Although the nonhuman orthograde primates included in this study use various locomotor modes (brachiation, arm-swinging, knuckle-walking), we observed no large differences in the expression patterns of the MHC isoforms according to locomotor mode, but we were unable to make statistical comparisons between nonhuman orthograde primate locomotor groups because of the small sample size. Interestingly, we observed significant differences in the expression patterns of the MHC isoforms between knuckle-walking orthograde primates and the arboreal quadrupeds and semiterrestrial quadrupeds pronograde primates, indicating that the electromyographic activity in the chimpanzee and the gorilla supraspinatus (Larson and Stern, 1987; Tuttle and Basmajian, 1978) is not related to a pronograde-like MHC expression pattern.

The modern humans in the present study had an MHC expression pattern similar to that of the other orthograde primates, with expression of all 3 isoforms and a higher proportion of the 2 fast MHC-II isoforms. However, the modern humans expressed a higher percentage of the MHC-IIx isoform and a correspondingly lower percentage of the MHC-IIa isoform. This higher expression of the fastest isoform may be due to the greater mobility and precision of the muscles of the upper extremity in modern humans, where the locomotor function has, to a large extent, been replaced by a manipulative function.

In conclusion, RT-PCR is a valuable technique for the molecular study of skeletal muscles and can complement information obtained via other techniques, such as electromyography, ATPase staining, and immunohistochemistry. We here observed molecular evidence of 2 different functional patterns in the supraspinatus muscle of primates, related to the anatomical pattern of modern humans and nonhuman orthograde vs. pronograde and to the locomotor modes of different species.

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6. Expression of myosin heavy chain isoforms in the human supraspinatus muscle. Variations related to age and sex.

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RESUMEN

Este estudio se cuantificó mediante *Real-Time PCR* (RT-PCR) la expresión de mRNA de las tres isoformas de la cadena pesada de la miosina (MHC) en 24 músculos supraespinosos de humanos modernos con el fin de determinar si corresponde a un músculo postural (con mayor expresión de la isoforma lenta MHC-I, apropiada para su función como estabilizador de la articulación glenohumeral) o a un músculo fásico (con mayor expresión de las isoformas rápidas MHC-II, adecuadas para actuar como elevador de la extremidad anterior). La muestra incluye individuos de diferentes edades y sexos con el fin de analizar la variabilidad de la expresión de MHC en relación con el síndrome subacromial y el debilitamiento de los músculos del manguito rotador.

En todas las muestras analizadas se observó una mayor expresión de las isoformas rápidas MHC-II (incluida la más rápida de todas, MHC-IIx) indicadora de la naturaleza elevadora del músculo supraespinoso (junto con el deltoides), capaz de rápidas contracciones pero poco resistente a la fatiga (Larsson & Moss 1993; Harridge *et al*. 1998), papel que también ha sido confirmado mediante estudios electromiográficos (Basmajian & de Luca 1985).

No se encontraron diferencias significativas en la expresión en relación con la edad o el sexo de los individuos, aunque sí se observaron diferencias entre categorías de edad por sexos. En las mujeres, la correlación negativa observada entre la edad y la expresión de la isoforma MHC-I, y la correlación positiva entre la edad y la expresión de la isoforma MHC-IIx, podrían ser indicativas de una reducción de la resistencia a la fatiga del músculo supraespinoso con

la edad. En los hombres no se observan estos cambios en la expresión de las isoformas MHC-I y MHC-IIx, sino un aumento de la expresión de la isoforma MHC-Ia con la edad.

Las diferencias observadas en la expresión de las isoformas de MHC en función de la edad y el sexo podrían explicar, al menos en parte, la mayor incidencia del síndrome subacromial en las mujeres de edad avanzada (Chard *et al*. 1991; Lehman *et al*. 1995), causado por el debilitamiento de los músculos del manguito rotador. Al debilitarse el manguito, el deltoides adquiere más importancia en la elevación de la extremidad anterior, lo que resulta en el desplazamiento de la cabeza del húmero y el aumento de la compresión del tendón del músculo supraespinoso contra el acromion, dañándolo (Wickiewicz 1994; Thompston *et al*. 1996; Chen *et al*. 1999).

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Expression of Myosin Heavy Chain Isoforms in the Human Supraspinatus Muscle: Variations Related to Age and Sex

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Key Words
MHC-I · MHC-II · mRNA · Myosin heavy chain isoforms · Shoulder · Subacromial impingement syndrome · Supraspinatus

Abstract

The contractile function of skeletal muscles is primarily regulated by the expression of myosin heavy chain (MHC) isoforms. Adult human skeletal muscles express three MHC isoforms (MHC-I, MHC-IIa and MHC-IIx). The muscles mainly expressing MHC-I are slow but resistant to fatigue, while those with major expression of MHC-IIa and MHC-IIx are fast and powerful but less resistant to fatigue. In this study, mRNA levels of the MHC isoforms were assessed in 24 human supraspinatus muscles by reverse-transcription polymerase chain reaction. The average expression of the MHC-I isoform was 36.72%, that of the MHC-IIa isoform was 33.52%, and the average expression of the MHC-IIx isoform was 29.76%. The higher average expression of the two MHC-II isoforms taken together (63.28%) indicates that the human supraspinatus muscle is a powerful, fast muscle with relatively low resistance to fatigue, in accordance with its role in the elevation of the upper extremity. In women, and more markedly in older women, the trend towards upregulation of the fast MHC-II isoforms and downregulation of the slow MHC-I isoform, which is absent in males, may improve our understanding of possible causes of the subacromial impingement syndrome.

Introduction

Together with the subscapularis, infraspinatus and teres minor muscles, the supraspinatus muscle forms part of the rotator cuff, which is the principal stabilizer of the glenohumeral joint [Michener et al., 2003; Ward et al., 2006; Lovering and Russ, 2008]. In addition to this stabilizing function, the supraspinatus muscle, along with the deltoid, with which it forms the upper unit described by Inman et al. [1944], elevates the upper extremity in the scapular plane [Inman et al., 1944; Basmajian and de Lucca, 1985; McMahon et al., 1995; Alpert et al., 2000; Halder et al., 2001]. The structure and function of the supraspinatus muscle warrants investigation since impairment in

Abbreviations used in this paper

MHC	myosin heavy chain
RT-PCR	reverse-transcription polymerase chain reaction
SAIS	subacromial impingement syndrome

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the supraspinatus tendon is the main feature of the subacromial impingement syndrome (SAIS) [Neer, 1983], the most frequent degenerative disorder affecting the human shoulder [Vecchio et al., 1995].

The characteristics of the skeletal muscles, such as contraction time, strength and resistance to fatigue, highly depend on the degree of expression of the different MHC isoforms in the muscle fibers [Botinelli and Reggiani, 2000]. Human skeletal muscles express three MHC isoforms (the slow MHC-I and the fast MHC-IIa and MHC-IIx, which are related to greater speed, greater strength and less resistance to fatigue, respectively). In addition to these three MHC isoforms, a gene encoding the fastest and least resistant isoform, MHC-IIb, has also been identified in humans [Weiss et al., 1999], but it is not expressed under normal conditions [Pette and Staron, 2000]. The slow postural muscles of the lower extremity, such as the soleus, highly express the slow MHC-I isoform, with a variable expression of the MHC-IIa isoform, the slower of the two fast MHC-II isoforms [Fitts et al., 1991; Baldwin, 1996; Fitts and Widrick, 1996; Schiaffino and Reggiani, 1996; Rivero et al., 1999; Talmadge, 2000]. In contrast, the fast muscles of the upper extremity express all three MHC isoforms in variable proportions [Larson and Moss, 1993; Harridge et al., 1998].

In the present study, we have quantified mRNA expression of the three MHC isoforms by reverse-transcription polymerase chain reaction (RT-PCR) in 24 human supraspinatus muscles obtained from cryopreserved corpses. The primary objective of this study was to determine if the expression of the three isoforms was similar to that of a postural muscle – with higher expression of the slow MHC-I, appropriate to its function as a stabilizer of the glenohumeral joint – or to that of a fast, powerful muscle – with higher expression of the fast MHC-II isoforms, suitable for its role in the elevation of the upper extremity [Larson and Moss, 1993; Harridge et al., 1998]. Furthermore, we reasoned that increased knowledge of MHC isoform expression in the supraspinatus muscle, including age- and sex-related variations, could improve our understanding of potential etiopathogenic mechanisms of SAIS related to the weakening of rotator cuff muscles.

Materials and Methods

Supraspinatus Muscle Samples

Muscle samples were obtained from 29 unfixed human cadavers from the Body Donation Service of the University of Barcelona and cryopreserved within 24–48 h of death. The shoulder regions of all cadavers were systematically dissected by the same investigator; after isolating and extracting the supraspinatus muscle, 3 samples were taken from the central area and frozen in saline solution. In order to avoid muscle area-based differences in MHC isoform expression, samples were obtained from the same area in all cadavers. One sample from each cadaver was used for mRNA quantification of the MHC isoform, and the remainder (2 samples) was stored for use in future studies. Samples from 5 cadavers were not included in the study due to macroscopic evidence of different types of pathologies. The 24 remaining cases included 13 males (aged 51, 60, 61, 66, 69, 72, 74, 76, 79, 84, 85, 88 and 91 years) and 11 females (aged 38, 44, 76, 81, 81, 83, 87, 91, 94, 97 and 98 years). The mean age of all the individuals was 76.1 years.

RNA Isolation and cDNA Synthesis

Total RNA from muscles was extracted using the commercial RNeasy mini kit (Qiagen, Valencia, Calif., USA) according to the manufacturer's protocol. The concentration, purity and amount of total RNA were determined by UV spectrophotometry, and the integrity and quality of RNA were assessed by electrophoresis on 1% agarose gel. RNA from samples was quantified in duplicate using a NanoDrop 1000 Spectrophotometer. cDNA was synthesized using a TaqMan reverse transcription reagent kit (Applied Biosystems, Foster City, Calif., USA). Reverse transcription was performed using 330 ng of total RNA in 10 μl of TaqMan RT buffer, 22 ml of 25 mM magnesium chloride, 20 μl dNTPs, 5 μl random hexamers, 2 μl RNAse inhibitor, 2.5 μl MultiScribe reverse transcription and RNA sample plus RNAse-free water, for a final volume of 100 μl, in the following thermal cycler conditions: 10 min at 25°C, 48 min at 30°C and 5 min at 95°C.

Gene Expression and Quantification by RT-PCR

Primers and probes were supplied by Applied Biosystems. Primers were labeled at the 5′ end with the reporter dye molecule FAM. MYH-I (Hs00165276_m1), MYH-IIa (Hs00430042_m1), MYH-IIx (Hs00428600_m1) and MYH-IIb (Hs00757977_m1) genes were analyzed. The 18S gene probe labeled at the 5′ end with the reporter dye molecule FAM (Hs99999901_s1) was used as housekeeping gene.

RT-PCR was performed in a total volume of 20 μl in the ABI Prism 7700 sequence detection system (Applied Biosystems). For each gene, all samples were run in duplicate for 40 cycles using the following Master Mix and thermal cycler conditions: 10 μl of the TaqMan universal PCR Master Mix, 1 μl of the primers and probes, 2 μl of the cDNA and 7 μl of the RNAse-free water for 2 min at 50°C, 10 min at 95°C, 15 s at 95°C and 1 min at 60°C. Genomic DNA was used as a negative control in each run. Fluorescent emission data were captured, and mRNA concentrations were quantified using the critical threshold value and $2^{-\Delta\Delta Ct}$. In order to avoid any possible effects of postmortem mRNA degradation, the mRNA values for each of the MHC isoforms were normalized using the endogenous gene 18S, which remains intact for up to 8 days after death in skeletal muscle [Bahar et al., 2007].

Statistical Analyses

The proportional expression of each MHC isoform (MHC-I, MHC-IIa and MHC-IIx) relative to the total expression of all MHC isoforms was calculated for each sample, and the expression of the two fast MHC-II isoforms taken together was compared to the expression of the slow MHC-I isoform. Average values were

Table 1. mRNA expression [means (SD)] of MHC isoforms in the supraspinatus muscle

Myosin isoforms	Total (n = 24)	Males (n = 13)	Females (n = 11)
MHC-I	36.72 (2.48)	36.26 (2.42)	37.28 (2.54)
MHC-IIa	33.52 (1.49)	33.99 (1.28)	32.96 (1.58)
MHC-IIx	29.76 (2.59)	29.75 (2.84)	29.76 (2.40)
MHC-II (IIa + IIx)	63.28 (2.48)	63.74 (2.42)	62.72 (2.54)

There was no significant difference in expression patterns between males and females.

computed for the whole study samples (n = 24). Differences between males and females were analyzed with the Mann-Whitney test. Age-related differences in gene expression between younger and older individuals, using mean patient age (76.1 years) as the cutoff point (73.5 for males and 79.1 for females), were analyzed with the Mann-Whitney non-parametric test, and the relationship between age and MHC isoform expression was assessed using the Spearman coefficients of correlation. Values of $p < 0.05$ were considered statistically significant. All statistical analyses were performed with SPSS version 14.

Results

The two fast isoforms (MHC-IIa and MHC-IIx) were expressed at a higher proportion than the slow isoform (MHC-I): 63.28 versus 36.72% (range 57.94–66.96 vs. 33.04–42.06%), respectively. However, when each isoform was considered separately (table 1), MHC-I was the most expressed (36.72%) followed by MHC-IIa [33.52% (range 29.97–36.10%)] and MHC-IIx [29.76% (range 24.97–34.74%)]. MHC-IIb was not expressed in any of the samples.

MHC expression followed the same pattern when age groups were considered. In samples from individuals aged 38–76 years, MHC-I was the most expressed isoform (37.30%) followed by MHC-IIa (33.03%) and MHC-IIx (29.66%), and again the two MHC-II isoforms taken together were expressed in a higher proportion (62.70%) than the MHC-I isoform. In individuals aged 79–98 years, MHC-I was again the most expressed (36.23%), followed by MHC-IIa (33.93%) and MHC-IIx (29.83%), and the two MHC-II isoforms, taken together, were also expressed in a higher proportion (63.77%).

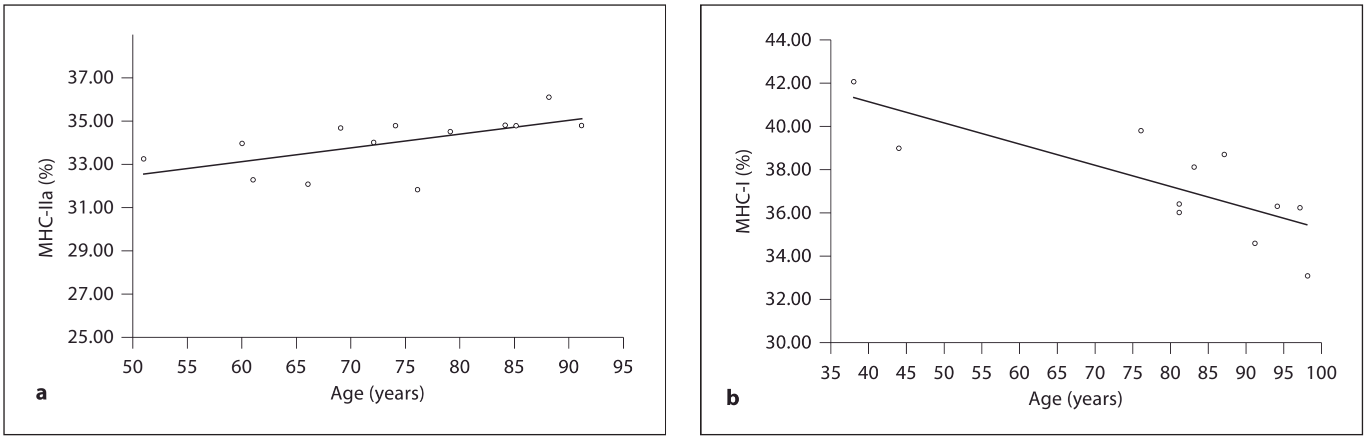
A similar pattern was observed when samples were grouped by sex. In males, MHC-I was expressed at a proportion of 36.26%, MHC-IIa at 33.99% and MHC-IIx at 29.75%. In females, MHC-I was expressed at 37.28%, MHC-IIa at 32.96% and MHC-IIx at 29.76%. In both males and females, the two MHC-II isoforms taken together were expressed at a higher proportion than MHC-I (males 63.74% and females 62.72%).

Although no significant differences in the overall relative expression of the three MHC isoforms were observed according to sex or age, different patterns of expression were identified within the subgroups of males and females according to age. In males, the expression of MHC-IIa was significantly higher in older subjects. In younger males, MHC-IIa was expressed at 33.38% (range 32.07–34.68%), while in older males it was expressed at 34.52% (range 31.82–36.10%; p = 0.046), but no changes were observed according to age in the expression of MHC-I (p = 0.475) or MHC-IIx (p = 0.253). In contrast, in females there was no change according to age in the expression of MHC-IIa (p = 0.414), but MHC-I expression decreased with age. In younger females, MHC-I was expressed at 40.28% (range, 38.98–42.06%), while in older females, it was expressed at 36.15% (range 33.04–38.68%; p = 0.014). In younger females, MHC-II isoforms were expressed at 59.72% (range 57.94–61.02%), while in older females, they were expressed at 63.85% (range 61.32–66.96%; p = 0.014). There was a nonsignificant trend towards increased expression of MHC-IIx in older females: 27.57% (range 27.16–27.97%) in younger females compared to 30.58% (range 27.03–34.08%) in older females (p = 0.066). The analysis of the correlation between myosin expression and age by sex group (table 2; fig. 1) showed a significant positive association between age and MHC-IIa expression in males (SCI = 0.71, p = 0.007; fig. 1a), a negative correlation between age and MHC-I expression in females (SCI = 0.79, p = 0.004; fig. 1b) and positive correlations between age and MHC-IIx expression (SCI = 0.62, p = 0.040) and between age and the expression of the two MHC-II isoforms taken together (SCI = 0.79, p = 0.004; fig. 1c) in females.

Table 2. Spearman correlation and significance [bilateral p value (in parentheses)] for non-parametric correlation analyses between age and percent mRNA expression of MHC isoforms in the supraspinatus muscle

MHC isoforms	Total sample (n = 24)	Males (n = 13)	Females (n = 11)
MHC-I	–0.251 (0.238)	–0.104 (0.734)	–0.788 *(0.004)*
MHC-IIa	0.252 (0.235)	0.709 *(0.007)*	0.082 (0.811)
MHC-IIx	0.163 (0.447)	–0.280 (0.354)	0.624 *(0.040)*
MHC-II (IIa + IIx)	0.251 (0.238)	–0.104 (0.734)	0.788 *(0.004)*

Significant p values are italicized.



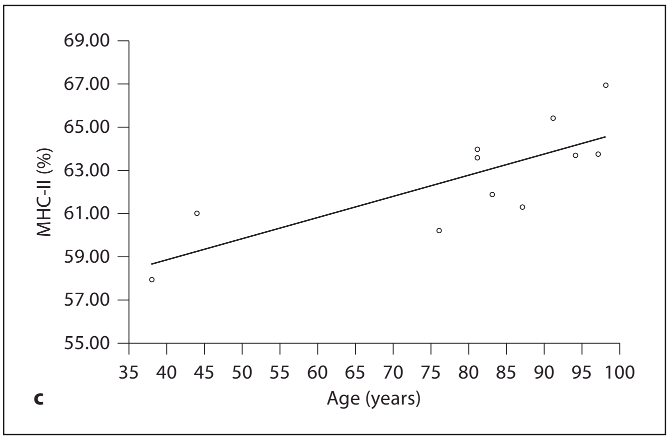


Fig. 1. Regression plots of age versus mRNA expression of MHC-IIa in 13 male cadavers (**a**); MHC-I in the supraspinatus muscle in 11 female cadavers (**b**) and MHC-II in 11 female cadavers (**c**).

Discussion

Previous studies (with smaller sample sizes) have already analyzed the presence of the MHC isoforms in supraspinatus muscle fibers. Using myofibrillar ATPase staining in three supraspinatus muscles, Srinivasan et al. [2007] identified 50% (±15%) of type-I fibers, 21% (±5%) of type-IIa fibers and 29% (±14%) of type-IIx fibers. Using immunohistochemistry, Lovering and Russ [2008] found 54% (±6%) of type-I fibers in 9 supraspinatus muscles. A marked difference in the percentages of fiber types exist between those identified by ATPase staining or immunohistochemistry and the percent of MHC isoforms obtained in the present study using RT-PCR. However, when Lovering and Russ [2008] quantified the protein levels of MHC isoforms by SDS-PAGE in 3 supraspinatus muscles, they found that the proportion of MHC-I expression was 33–47%, that of MHC-IIa was 19–42%, and that of MHC-IIx was 17–35%. These results are along the lines of our findings: 33–42% MHC-I, 30–36% MHC-IIa and 25–35% MHC-IIx. Both SDS-PAGE and RT-PCR are indicative of the higher expression of the fast MHC-II isoforms compared with the slow MHC-I isoforms in the human supraspinatus muscle, although MHC-I shows the highest expression when the three isoforms are considered separately, followed by MHC-IIa and finally by MHC-IIx. The proportion of type-I fibers observed by ATPase staining [Srinivasan et al., 2007] and immunohistochemistry [Lovering and Russ, 2008], 50 and 54%, respectively, is higher than the 36.72% observed by us for MHC-I expression using RT-PCR. The higher values observed by the former studies could possibly be affected by the presence of hybrid fibers expressing both MHC-I and MHC-IIa [Smerdu et al., 1994].

The higher expression of the fast MHC-II isoforms, including the fastest (MHC-IIx), which was observed in the present study and also by others [Lovering and Russ, 2008], may reflect the functionally powerful nature of the supraspinatus muscle, which is capable of fast contractions but has low resistance to fatigue [Larson and Moss, 1993; Harridge et al., 1998]. This interpretation of the supraspinatus muscle highlights its function in the elevation of the upper extremity, where, together with the deltoid muscle, it forms part of the upper unit [Inman et al., 1944]. This role of the supraspinatus has also been verified through electromyographic studies [Basmajian and de Luca, 1985].

We have found no significant differences in the relative expression of the MHC isoforms according to age or sex, though differences between age categories by sex groups were identified: MHC-IIa expression was higher in older males, whereas MHC-I expression was lower in older females and MHC-II expression was higher in older females. These results confirm those of previous studies [Balagopal et al., 2001; Short et al., 2005; Toth et al., 2005], where the expression of MHC-II isoforms increased with age. The major difference in our findings is that we have observed a significant decrease in the expression of the MHC-I isoform in older females. In contrast, other studies have reported a lack of age-related changes in MHC expression [Marx et al., 2002; Toth and Tchernof, 2006]. However, these studies were carried out in the vastus lateralis muscle, which has different functional requirements and, thus, a different MHC expression pattern than the muscles of the upper extremity. In the vastus lateralis, an overall higher expression of MHC-I, and scarce or null expression of MHC-IIx has been described [Botinelli and Reggiani, 2000]. We propose that the functional demands on the upper extremity muscles, including the supraspinatus, may lead to different age-related patterns in the expression of MHC isoforms.

In females, the negative correlation between age and MHC-I expression and the positive correlation between age and MHC-IIx expression might be indicative of a tendency towards a lower resistance to fatigue of the supraspinatus muscle. In males, these changes in MHC-I and MHC-IIx expression were not observed, and the age-related increase observed for MHC-IIa expression implies a higher resistance to fatigue of the supraspinatus muscle in males. The weakness of the rotator cuff muscles, including the supraspinatus, has been postulated as an etiopathogenic cause of SAIS [Jerosh et al., 1989; Warner et al., 1990; Brox et al., 1993; Bartolozzi et al., 1994; Leroux et al., 1994; Hawkins and Dunlop, 1995; Reddy et al., 2000] because it entails a greater role for the deltoid in the elevation of the upper extremity, resulting in a greater upward movement of the humeral head and an increased compression of the supraspinatus tendon against the acromion, which will gradually injure the supraspinatus tendon [Wickiewicz, 1994; Thompson et al., 1996; Chen et al., 1999]. The observed differences in MHC isoform expression with age between males and females might be responsible, at least in part, for the higher incidence of SAIS in older women [Chard et al., 1991; Lehman et al., 1995]. Future studies are warranted to determine if the changes we have observed in the mRNA expression of the MHC isoforms correspond to similar changes in protein expression, since there is not always a good correlation between mRNA and protein expression [Toth and Tchernof, 2006].

Nevertheless, SAIS is a multifactorial syndrome, and contributory factors include inflammation of the tendons and the subacromial bursa [Ogata and Uhthoff, 1990; Banas et al., 1995; Toivonen et al., 1995; Tuite et al., 1995; Paletta et al., 1997], as well as the morphology of the acromion and the coracoacromial arch [Farley et al., 1994; Bigliani and Levine, 1997]. For this reason, our results can only help explain one of the many possible causes of SAIS – the age-related weakening of the rotator cuff muscles. Further studies on the other rotator cuff muscles (the subscapularis, infraspinatus and teres minor muscles) investigating age-related MHC isoform changes similar to those we have noted in the supraspinatus are required to confirm the relationship between the expression of MHC isoforms and the etiopathogenesis of SAIS.

Finally, some precautions need to be considered since the samples were obtained from cadavers, which implies that the average age of the samples was high and the control for previous pathologies was not always possible; only 2 young individuals could be analyzed. Thus, only linear regression could be performed. A larger sample, with all age groups represented, might show whether a nonlinear model will better fit the data or not. Nevertheless, the reliability of the quantification of mRNA expression by RT-PCR and the significant amount of studied individuals allow us to hypothesize that age-related changes in myosin expression may underlie sex-related differences in some muscles like the supraspinatus.

The present study on the expression of MHC isoforms in the supraspinatus muscle can shed new light on the characteristics of this muscle, including its age- and sex-related molecular variations. Our results can complement previous findings using different techniques, such as the study of the supraspinatus muscle architecture [Ward et al, 2006], the physiological cross-sectional area of the muscle fibers [Srinivasan et al., 2007], electromyography [Basmajian and de Luca, 1985] and muscle fiber types [Lovering and Russ, 2008], and can help increase our understanding of the functional aspects of the supraspinatus and provide insights into one potential cause of SAIS.

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