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CONTENIDO

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EVOLUTION OF ARM SIZE IN THEROPOD DINOSAURS: A DEVELOPMENTAL HYPOTHESIS

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RESUMEN

Entre especies de dinosaurios terópodos existe una tendencia a la disminución de la proporción de los brazos a medida que aumenta el tamaño. (Húmero=0.3876fémur$^{0.6807}$, R(r^2)=0.89). Esta tendencia puede reflejar descendencia común de un ancestro en el que el brazo crecía alométricamente más lento que el cuerpo. La conservación de este patrón ontogénico en terópodos de gran tamaño pudo ser admitida ya que la falta de funcionalidad de los brazos en la depredación es compensada por el tamaño corporal. Esta hipótesis predice el descubrimiento en el registro fósil de secuencias ontogénicas de terópodos en que los estadíos más tempranos presentan brazos proporcionalmente mayores que los estadios más tardíos.

Palabras clave: Dinosaurios, Terópodos, Alometría, Brazo, Ontogenia

ABSTRACT

Among theropod species the arm tends to become proportionately smaller as size increases. (Humerus=0.3876femur$^{0.6807}$, R(r^2)=0.89). This trend may reflect common descent from an ancestor in which the arm grew alometrically slower than the body. Conservation of this developmental trend could have been allowed in large theropods since arms not functional in predation are compensated by a large body size. This hypothesis predicts the fossil record will show developmental sequences of theropods in which earlier stages show arms proportionately longer than those of later stages.

Key words: Dinosaurs, Theropods, Allometry, Arm Size, Ontogeny

INTRODUCTION

The carnivorous dinosaurs (Theropoda) include the first dinosaurs known and evolved a striking diversity of forms during their 160 million years of existence. The theropods can be considered the only dinosaurs to have survived the cretaceous-tertiary extinction, as a majority of authors regard them to be the ancestors of birds. Among theropods those best known are large species famous for their surprisingly small-looking arms. Less famous though is the fact that many smaller theropod species show arms proportionately larger than their giant counterparts. The following paper evaluates the existence of a trend among theropods species to show proportionately smaller arms at larger sizes. Such evolutionary trend can be explained by a developmental hypothesis ultimately testable if ontogenetic sequences of theropods were to be found in the fossil record.

METHODS

This study considers bibliography-obtained data from 26 specimens whose preservation has made it possible to measure humerus and femur length (see attached data). *Archaeopteryx lithographica* can be included as a derived theropod. The femur was chosen as a rough indicator of size and a comparable unit among all theropods. Body length correlates directly with femur length (lineal regression R= 0.96, data not shown) but femur length is preferred since body length is subject to variation in the number of vertebrae, and complete enough specimens are less frequent. Body mass is not reliable since estimates vary widely among authors.

When humerus length data could not be obtained from bibliography describing the specimens it was deduced from scaled skeletal restorations drawn by Paul (1987, 1988), where humerus and femur are drawn in the sagittal plane therefore reflecting the actual length of these bones. For a complete description of the methodology used by Paul in elaborating these restorations, see Paul 1987. The drawings were measured from enlarged photocopies using a calliper to reduce error.

Humerus and femur length were contrasted by a multiplicative regression obtaining a curve of the form $y = ax^b$ and its respective determination coefficient ($R=r^2$). Hypotheses on significance of r (correlation coefficient) were tested using Student's test to a 99.9% of certainty.

RESULTS-DISCUSSION

The determination coefficient R=0.895 reveals a marked tendency in theropod dinosaurs to show proportionately smaller humeri at higher femur sizes, as described in the equation by $b<1$ (b=0.6807); r is significantly different from 0 ($t=14.55 > t_{critical} = 3.707$, see figure). This result is not altered by exclusion of *A. lithographica* (b= 0.71, R= 0.85). As a hypothesis for explaining such an intriguing general trend among species, I propose it to reflect common descent from an ancestor in which the arm grew slower than the body. Conservation of this developmental trend could have been allowed in large theropods since arms not functional in predation are compensated by size. A prediction of this developmental hypothesis is that most theropods will show proportionately larger humeri at developmental stages earlier than those showing proportionately smaller humeri. Since well-preserved developmental sequences for species of non-theropod dinosaurs have been found (Horner and Weishampel 1988) it is possible the fossil record will allow this hypothesis to be put to test. Since development is subject to evolution it is not unexpected that in 160 million years of evolution some theropods fall out of the tendency, such as the ornithomimid *Gallimimus bullatus*, a long-armed large species. The pattern is best seen in tetanuran theropods excluding ornithomimids (b= 0.66, R= 0.94).

The hypothetical presence of a "negative" alometry in theropod arm growth provides a new explanation for the evolution of short arms in large theropods and is consistent with proposals of paedamorphosis at bird origins for the evolution of long arms in *A. lithographica* (Long and Mcnamara 1995; Thulborn 1985, as quoted in Long and Mcnamara 1995).

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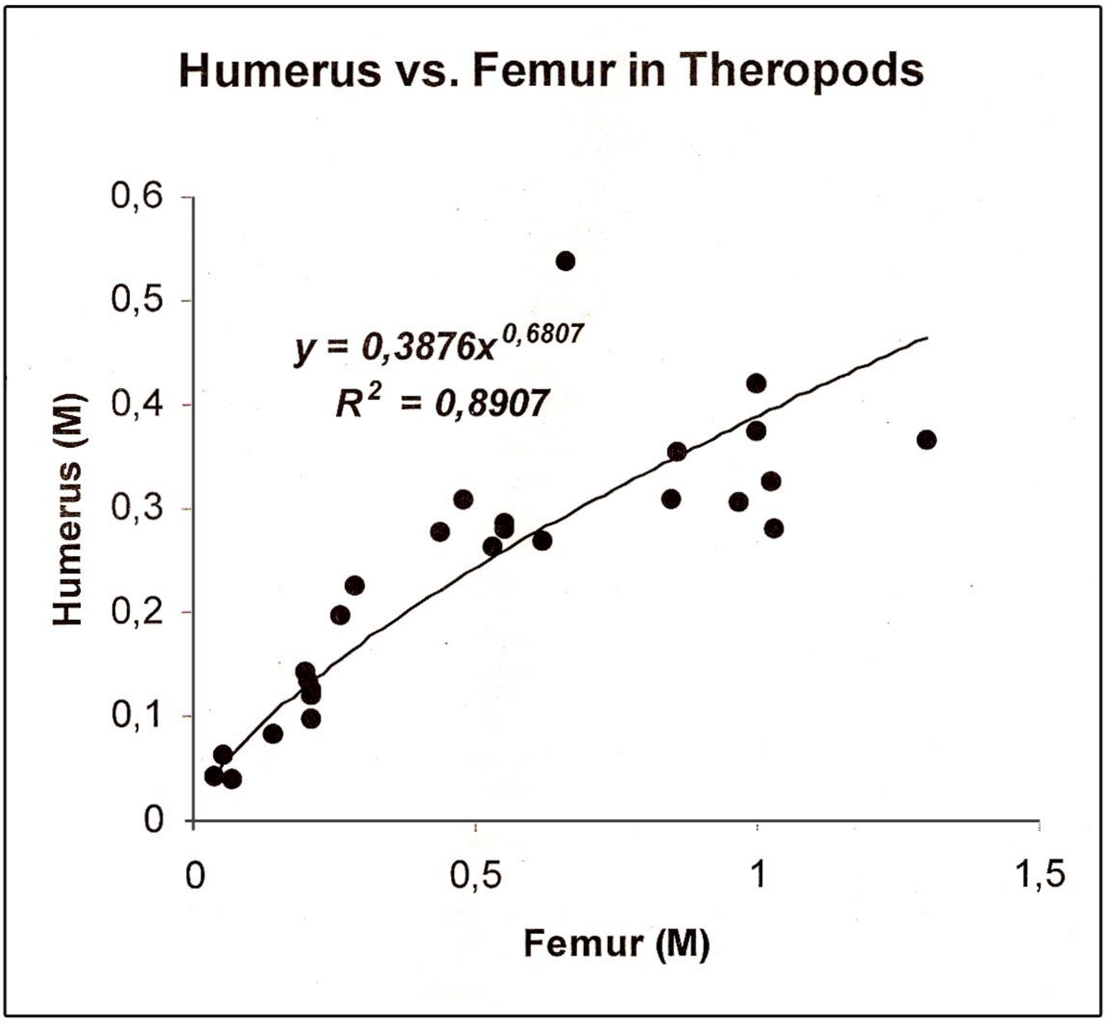

Taxon	Femur length (M)	Humerus length (M)	Reference
Archaeopteryx lithographica (J)	0.037	0.042	Paul 1988
Archaeopteryx lithographica (SA)	0.053	0.064	Paul 1988
Sinornithoides youngi	0.140	0.083	Russel and Dong 1993
Velociraptor mongoliensis	0.200	0.143	Paul 1988
Ornitholestes hermani	0.207	0.127	Paul 1988
Oviraptor philoceratops	0.262	0.196	Paul 1988
Deinonychus antirrhopus	0.284	0.226	Paul 1988
Ornithomimus edmontonicus	0.435	0.276	Paul 1988
Struthiomimus altus	0.480	0.310	Paul 1988
Piatnizkysaurus floresi	0.552	0.280	Bonaparte 1996
Gallimimus bullatus	0.660	0.536	Paul 1988
Allosaurus fragilis	0.850	0.310	Madsen 1976
Tarbosaurus bataar	0.970	0.305	Paul 1988
Allosaurus atrox	0.860	0.354	Paul 1987
Albertosaurus libratus	1.025	0.327	Galton and Jensen 1978
Daspletosaurus torosus	1.000	0.373	Galton and Jensen 1978
Tyrannosaurus rex	1.300	0.367	Paul 1988
Compsognathus longipes	0.067	0.039	Ostrom 1978
Coelophysis rhodesiensis	0.208	0.097	Paul 1988
Coelophysis bauri	0.210	0.120	Colbert 1964
Coelophysis bauri	0.203	0.134	Colbert 1964
Ceratosaurus nasicornis	0.620	0.268	Madsen 1976
Dilophosaurus wetherilli	0.550	0.285	Welles 1987
Baryonix walkerii	1.000	0.419	Paul 1987
Carnotaurus sastrei	1.030	0.279	Bonaparte 1996
Elaphrosaurus bambergi	0.529	0.262	Paul 1988

SA is subadult and J is juveniles.