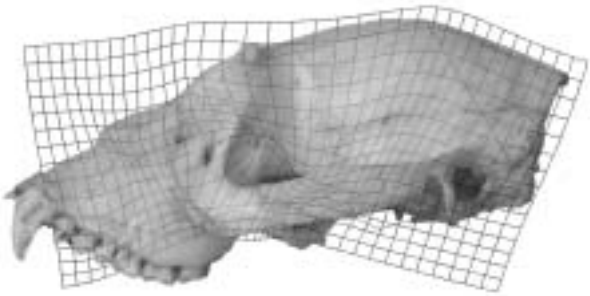
SHAPE MEETS FUNCTION: STRUCTURAL MODELS IN PRIMATOLOGY

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Locomotor adaptations of *Plesiadapis tricuspidens* and *Plesiadapis n. sp.* (Mammalia, Plesiadapiformes) as reflected on selected parts of the postcranium

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Summary – *Plesiadapis is one of the best-known Plesiadapiformes, a group of Archontan mammals from the Late Paleocene-Early Eocene of Europe and North America that are at the core of debates concerning primate origins. So far, the reconstruction of its locomotor behavior has varied from terrestrial bounding to semi-arboreal scansoriality and squirrel-like arboreal walking, bounding and claw climbing. In order to elucidate substrate preferences and positional behavior of this extinct archontan, the present study investigates quantitatively selected postcranial characters of the ulna, radius, femur, and ungual phalanges of P. tricuspidens and P. n .sp. from three sites (Cernay-les-Reims, Berru, Le Quesnoy) in the Paris Basin, France. These species of Plesiadapis was compared to squirrels of different locomotor habits in terms of selected functional indices that were further explored through a Principal Components Analysis (PCA), and a Discriminant Functions Analysis (DFA). The indices treated the relative olecranon height, form of ulnar shaft, shape and depth of radial head, shape of femoral distal end, shape of femoral trochlea, and distal wedging of ungual phalanx, and placed Plesiadapis well within arboreal quadrupedal, clambering, and claw climbing squirrels. In a comparable way, the PCA and the DFA ordered Plesiadapis with arboreal squirrels well away from terrestrial squirrels. It seems clear that P. tricuspidens, one of the largest plesiadapiforms, was a committed arborealist, most likely employing frequent arboreal quadrupedal walk and clamber along with claw climb on vertical supports. These findings corroborate to the arboreal nature of the archontan radiation, and will help working out scenarios for the acquisition of primate postcranial characteristics.*

Keywords – Plesiadapis tricuspidens, *postcranium*, *locomotor behavior*, *paleoprimatology*, *France*.

Introduction

The Plesiadapiformes is a morphologically primitive group of eutherian mammals, which diversified in many families in both Eurasia and North America during the Late Paleocene-Early Eocene. Plesiadapiformes form a clade along with the orders of Primates, Scandentia, Dermoptera, and Chiroptera to the supraordinal grouping of Archonta. However, the exact phylogenetic position of this group has risen debates. Plesiadapiformes were once considered as the most archaic members of the order Primates (Simpson, 1935; Gingerich, 1976; Szalay & Delson, 1979). More recently, Beard (1990; 1993) and Kay *et al*. (1990) suggested that Plesiadapiformes should be considered as a suborder of Dermoptera, proposing the mirorder Primatomorpha to lump the two sister groups of Primates-Dermoptera. Recent discoveries concur to the fact that Plesiadapiformes could share the latest common ancestor with Euprimates, the Primates of modern aspect (Szalay *et al*., 1975; Bloch & Silcox, 2001; Bloch & Boyer, 2002; Sargis, 2002a, b; Silcox, 2003), and might return within a redefined order Primates (Silcox, 2002).

However, this may not be the case, with Tupaiidae being the sister group of Euprimates (Godinot, in press).

Given the key position of Plesiadapiformes in the debate concerning the origins of Primates, it is important to assess the positional diversity of this group of mammals. For this purpose, postcranial elements help to assess the morphological and locomotor diversity of these Paleogene forms, as well as establish the phylogenetic relationships between Plesiadapiformes, Euprimates, Scandentia, Dermoptera, and Chiroptera (Szalay *et al*., 1975; Szalay & Dagosto, 1980; Beard, 1993; Szalay & Lucas, 1996; Bloch & Boyer, 2002; Sargis, 2002b; Godinot, in press). One of the best known plesiadapiforms is *Plesiadapis* (family *Plesiadapidae*) and more particularly the species *P. tricuspidens* with numerous postcranial remains from two sites in the Paris Basin, France (Russell, 1964; Szalay *et al*., 1975; Szalay & Delson, 1979; Beard, 1993; Godinot *et al*., 1998). The locomotor reconstruction of this species, whose body weight is estimated at 2,160 gr., has been debated. Gingerich (1976) noted that P. tricuspidens resembles more living rodents in postcranial proportions and is distinguished from arboreal scramblers, such as squirrels, by its larger intermembral and lower crural indices, implying the lack of long tibiae necessary for squirrel-like scansorial locomotion. On the other hand, Russell (1964) had found similarities in the morphology of the claws with those of gliding mammals, and proposed arboreal climbing habits only for escape. Napier & Walker (1967) suggested that *Plesiadapis* was rodent-like and quadrupedal most likely resembling tree shrews or squirrels in locomotor habits. Szalay *et al*. (1975) found many characters of the forelimb and hind limb that would suggest a squirrel-like scansorial way of climbing on vertical trunks or arboreal quadrupedal walking on smaller supports with no great ability for agile jumping between terminal branches. In a detailed study of the humerus, Szalay & Dagosto (1980) observed features that reflect increasing pronosupinatory movements implying an arboreal way of life. More recently, Jouffroy *et al*. (1991) found forelimb proportions that were closer to scansorial and vertically clinging callitrichids, while Godinot & Beard (1991) found that the morphology of the phalanges suggested an arboreal way of life using powerful driving of the claws into the support.

In this context, we studied selected features of the postcranium of *Plesiadapis* tricuspidens and a new early Eocene species (*Plesiadapis* n. sp.) from three localities in the Paris Basin, France, in order to determine any functional implications of support preference, and positional (locomotor-postural) behavior. The understanding of locomotor habits of *Plesiadapis* is essential in shedding light on the evolution of locomotor diversity within the Archonta, as well as in the understanding of locomotor scenarios for the origin of Euprimates. This euprimate morphotype locomotor mode is debated, being reconstructed either as arboreal grasp-leaping (Szalay & Dagosto, 1980; Dagosto, 1983, 1993; Szalay & Lucas, 1996; Gebo *et al*., 2001) or as arboreal quadrupedalism and climbing (Godinot & Jouffroy, 1984; Ford, 1988; Godinot, 1991).

Material and methods

The fossil material of *Plesiadapis tricuspidens* and *P. n. sp.* examined in this study is shown in Table 1. All the material is housed in the collections of the Institut de Paléontologie of the Muséum National d'Histoire Naturelle in Paris (MNHN). The fossil postcranial elements studied were excavated from three localities of the Paris Basin: the Cernay-les-Reims and Berru localities of Thanetian (Late Paleocene) age, and the Le Quesnoy locality of Sparnacian (Early Eocene) age. Despite pertaining to a new species of *Plesiadapis*, defined on dental characters (Godinot *et al*., 1998; Godinot *et al*., submitted), postcranials from Le Quesnoy have the same size and morphology as those of *P. tricuspidens*, and they were consequently added to increase our sample of *Plesiadapis* limb bones.
The extant comparative material was composed of recent squirrels (*Sciuridae, Rodentia*) housed in the collections of the Laboratoire d'Anatomie Comparée of the MNHN. Recent squirrels were chosen for several reasons: (a) the positional

Tab. 1 - Fossil postcranial elements of* Plesiadapis tricuspidens *and* P. n. sp. *examined in this study (MNHN: Muséum National d'Histoire Naturelle, Paris, France). The asterisk indicates recently discovered material that is not catalogued yet.

Postcranial Element	Catalog numbers (MNHN)
Ulna	Proximal: R411, R542, R546, R615, R2527
	Proximal with broken olecranon: R443, Berru*
Radius	Complete: R550
	Proximal: R553, R597
Femur	Complete: BR-16-L, R407, R408, R444, R446
	Distal: Berru*, Le Quesnoy*
Ungual Phalanges	Complete: R613, R5361, R5370, R5381, Berru* (n=3)
	Le Quesnoy* (n=7)
	Distal edge broken: R549, R612, R5309

behavior of *Plesiadapis* was frequently compared to that of either terrestrial marmots (Gingerich, 1976) or scansorial squirrels (Szalay *et al*., 1975; Godinot & Beard, 1991); (b) squirrels are among the most primitive rodent families and are postcranially conservative (Emry & Thorington, 1982); and (c) within the same family, there are species that occupy quite divergent niches ranging from almost exclusively arboreal forms, to entirely terrestrial and semifossorial ones (Nowak, 1991). Thus, based on bibliographic reports on the locomotor and postural habits of squirrel species, we categorized three locomotor groups: (i) arboreal forms, that engage frequently in arboreal quadrupedal walking, clambering, and claw climbing; (ii) scansorial forms, that practice arboreal walking, claw climbing, and terrestrial bounding; and (iii) terrestrial forms, that employ terrestrial bounding, and digging (Tab. 2). These distinct locomotor behaviors are composed of limb movements that are biomechanically linked to regional functions. In turn, these functions can be firmly associated with certain morphological traits that facilitate or enable them. These traits can be detected by comparing phylogenetically close animals that engage in different behaviors (Lauder, 1995). In this way, a preliminary qualitative study of a large array of characters on the postcranium of these three locomotor groups revealed important morphological differences in certain characters. These characters were quantitatively expressed as linear measurements that are described in detail in Table 3. Subsequently, these measurements were used to calculate indices of functional significance (Tab. 4). These indices were selected to provide statistical significance between the different groups and many of them followed previously published functional indices (van Valkenburgh, 1987; Ford, 1988; Sargis, 2002 c,d). All calculated indices were plotted against the logarithm of body weight to test for possible correlations (Zar, 1996). Unplanned paired comparisons of means between different groups were performed with non-parametric Mann-Whitney U-tests using a criterion of $p<0.05$ (Zar, 1996).

The relative position of *Plesiadapis* in respect with the three functional groups was further explored with two additional analyses: (a) Principal Components Analysis, and (b)

Tab. 2 - Number of specimens, substrate category, and positional behavior of the extant comparative postcranial material.

Genus	n	Substrate category	Positional behavior
Ratufa	3	arboreal	Arboreal quadrupedalism/clamber/ claw climb
Callosciurus	1	arboreal	Arboreal quadrupedalism/clamber/ claw climb
Petaurista	5	arboreal/glider	Arboreal quadrupedalism/clamber/ claw climb/glide
Sciurus	8	scansorial	Arboreal quadrupedalism/claw climb/terrestrial bound
Protoxerus	1	scansorial	Arboreal quadrupedalism/claw climb/terrestrial bound
Heliosciurus	3	scansorial	Arboreal quadrupedalism/claw climb/terrestrial bound
Funambulus	2	scansorial	Arboreal quadrupedalism/claw climb/terrestrial bound
Xerus	3	terrestrial	Terrestrial bound/dig
Spermophilus	4	terrestrial	Terrestrial bound/dig
Marmota	2	terrestrial	Terrestrial bound/dig

Discriminant Functions Analysis. In the Principal Components Analysis (PCA), we created a matrix with adjusted indices (i.e. divided by the cubic root of body weight) in a way that eliminated the direct influence of size. The advantage of the PCA lies in the efficient projection of species and indices in a multidimensional space into fewer dimensions, represented by the first three axes (Factors or Principal Components), that minimize the relative distortion of distances (ter Braak, 1995). Having assessed the position of *Plesiadapis* through the study of individual indices and the PCA, we wanted to test the robustness of its position within a certain functional group and those indices that contributed most to that assignment. For these reasons, we performed the Discriminant Functions Analysis (DFA), using adjusted indices. The advantage of this procedure lies in the output of a set of discriminant functions that are based on those indices that are responsible for the best discrimination between the studied groups (ter Braak, 1995). All analyses were run with SPSS 8.0.

Results

Ulna

Among the Sciuridae examined, the relative height of the olecranon process was not correlated to body weight. The olecranon process of *Plesiadapis* is not particularly high but rather quadrangular and robust in overall shape. It approximates the condition found in most scansorial squirrels, and especially *Protoxerus* that possess a relatively low and thick olecranon (Tab. 5; Z=0.24, p=0.807). Arboreal sciurids possess relatively shorter but not significantly different olecrana (Tab. 5; Z=1.05, p=0.291). In contrast, the terrestrially adapted squirrels have significantly higher and mediolaterally narrower olecranon processes (Tab. 5; Z=-1.93, p=0.048; arboreal vs. terrestrial: Z=-2.39, p= 0.016).

The relative form of the ulnar shaft was not correlated to body weight. The form of the shaft in *Plesiadapis* is moderately robust and relatively compressed mediolaterally, bearing values similar to arboreal squirrels (Tab. 5; Z=-0.08, p=0.935). On the other hand, terrestrial forms appear to possess more robust and significantly less compressed shafts (Tab. 5; Z= -2.23, p=0.025; arboreal vs. terrestrial: Z= -2.12, p=0.027).

Radius

The relative shape of the radial head was not correlated to body weight. The radial head of *Plesiadapis* is ovoid in shape and resembles more to the condition seen in arboreal squirrels (Tab. 6; Z= -0.77, p= 0.438). In overall form it is particularly reminiscent of Ratufa. In contrast, more

Tab. 3 - Measurements on postcranial elements of Plesiadapis and extant rodents. The measurements are comparable to those reported in van Valkenburgh (1987), Ford (1988), and Sargis (2002cd).

Measurements	
Ulnar olecranon height:	proximal edge of olecranon to pr oximal edge of sigmoid cavity.
Ulnar sigmoid height:	proximal edge of sigmoid cavity to di stal edge of sigmoid (coronoid process)
Ulnar shaft mediolateral width:	medial edge to lateral edge at midshaft
Ulnar shaft anteroposterior breadth:	anterior edge to posterior edge at midshaft
Radial head width:	anterior edge of head to po sterior edge at proximal view
Radial head length:	medial edge of the head to lateral edge at proximal view
Radial head fossa depth:	proximal edge of head to deepest point inside the fossa
Distal femoral end height:	maximal height from trochlear ridges to posterior edge of condyles at distal view
Femoral biepicondylar width:	medial edge of medial condyle to lateral edge of lateral condyle at distal view
Femoral trochlea height:	distal edge of condyle to proximal extent of groove at anterior view
Femoral trochlea width:	medial trochlear ridge to lateral trochlear ridge at distal edge of anterior view
Ungual base height:	dorsal edge to ventral edge at the base of the shaft of ungual phalanx
Maximal height of ungual phalanx:	dorsal edge to ventral edge at midshaft of ungual phalanx

Tab. 4 - Calculated indices based on the selected measurements on the postacranial elements of Plesiadapis and extant sciurids.

Calculated Indices
Relative Olecranon Height = (olecranon height / sigmoid cavity height) x 100
Form of Ulnar Shaft = (shaft mediolateral width / shaft anteroposterior breadth) x 100
Radial Head Shape = (radial head width / radial head length) x 100
Radial Head Depth = head depth / (head length x head width)
Form of Distal Femoral End = (distal end height / biepicondylar width) x 100
Relative Form of Trochlea = (trochlea width / trochlea height) x 100
Distal Wedging of Ungual Phalanx = (maximal height of ungual / ungual base height) x 100

Tab. 5 - Median, lower and upper quartiles, and range of values of the calculated indices on ulna.

	n	median	quartiles	range
Relative Olecranon Height = (olecranon height / sigmoid cavity height) x 100				
Plesiadapis	5	88.16	86.15-96.05	38.05
Arboreal	7	85.71	69.70-92.31	33.39
Scansorial	7	85.00	79.59-97.51	33.61
Terrestrial	3	122.73	--	22.73
Form of Ulnar Shaft = (shaft mediolateral width / shaft anteroposterior breadth) x 100				
Plesiadapis	5	50.94	50.00-53.97	14.49
Arboreal	7	52.34	43.40-59.26	19.18
Scansorial	7	44.83	43.33-50.00	10.98
Terrestrial	3	58.18	--	6.45

terrestrially adapted rodents possess elongated radial heads resulting in significantly lower radial head shape indices (Tab. 6; Z=1.93, p= 0.042; arboreal vs. terrestrial: Z= -2.14, p= 0.032).

The relative depth of the capitular fossa on the proximal end of the radius was not correlated to body weight. In *Plesiadapis*, the capitular fossa on the proximal end of the head is relatively well excavated in a subspheroid concave way with a similar morphology also found in Ratufa. Most arboreal, scansorial, and gliding squirrels appear to have deeper fossae but not in a significant way (Tab. 6; arboreal: Z= -1.16, p= 0.245; scansorial: Z= -1.39, p= 0.164). In contrast, terrestrial forms bear significantly shallower facets that have an even flatter rather than concave aspect (Tab. 6; Z=-2.13, p= 0.037; arboreal vs. terrestrial: Z=-2.12, p= 0.034).

Femur

The relative shape of the distal femoral end was not correlated to body weight. The distal femoral end of *Plesiadapis* is relatively anteroposteriorly low and mediolaterally wide, presenting the lowest index values (Tab. 7). A similar morphology is encountered in arboreal and, to a lesser extent, scansorial squirrels but they are relatively higher (Tab. 7; Z= -2.36, p=0.018). In contrast, terrestrial squirrels bear significantly mediolaterally narrower and anteroposteriorly higher distal ends (Tab. 7; Z= -3.24, p= 0.001; arboreal vs. terrestrial: Z= -2.71, p= 0.006).

The relative form of the femoral trochlea was positively correlated to body weight (R=0.426, F=0.18, p=0.006). The femoral trochlea, located in the anterior surface of the distal femur, is low and wide in *Plesiadapis*, and is similar to the overall morphology that characterizes arboreal deliberate walking and climbing mammals (*Ratufa*, *Potos*, *Perodicticus*; arboreal: Z=0.63, p=0.522). This morphology is further coupled with a wide and very shallow patellar groove that is similar to that of *Ratufa*, *Potos* and *lorisids*. Compared to *Plesiadapis*, scansorial squirrels possess significantly higher trochleae (Tab. 7; Z= -2.47, p=0.013). On the other hand, terrestrial squirrels possess much narrower and higher trochleas, resulting in significantly low trochlea form index values (Tab. 7; Z= -3.09, p=0.002; arboreal vs. terrestrial: Z=2.71, p= 0.006). The morphology of terrestrial forms is further charac-

terized by a deeper groove that bears relatively prominent lips.

Ungual phalanx

The distal wedging of the ungual phalanx was positively correlated to body weight (R=0.494, F=0.244, p=0.001). In *Plesiadapis*, the ungual phalanges are particularly dorsoventrally high and mediolaterally compressed, curving gently distally to a sharp point. This morphology is characterized by relatively high values for the distal wedging index (Tab. 8). This general outline is very similar to arboreal squirrels, such as Ratufa (Tab. 8; Z=0.22, p=0.825). On the other hand, scansorial squirrels possess significantly shallower unguals that bear a sharp distal point too (Table 8; Z=2.52, p= 0.011). Lastly, terrestrial forms possess even shallower ungual phalanges that give significantly low index values (Tab. 8; Z=3.43, p= 0.000; arboreal vs. terrestrial: Z=3.41, p= 0.000).

Principal Components Analysis (PCA)

The results of the PCA of the adjusted indices are shown in Table 9 and Figure 1. The first Factor accounted for 94.7% of total variance, and the second for 3.8% (Tab. 9). These factors were responsible for separating three distinct groups that coincided more or less with the locomotor groups of squirrels based on substrate preferences. More specifically, *Plesiadapis* was ordered with *Petaurista*, *Protoxerus*, and *Ratufa*. The majority of scansorial squirrels were located near this grouping. Lastly, the terrestrial *Marmota*, *Spermophilus*, and *Xerus* were ordered far apart (Fig. 1). Along factor 1, *Plesiadapis*, arboreal, and scansorial species were ordered by the relative height of the olecranon process and the shape of the femoral distal end, whereas terrestrial species were ordered by the depth of the radial head (Tab. 9). Along factor 2, *Plesiadapis*, arboreal, and scansorial forms were ordered by the radial head shape and the distal wedging of the ungual phalanx, while terrestrial forms were ordered by the relative olecranon height (Tab. 9).

Discriminant Functions Analysis (DFA)

The results of the DFA further supported the position of *Plesiadapis* within arboreal squirrels. Functions 1 and 2 were highly significant (p=0.004), and the first function accounted for 84% of data variability (Tab. 10). Along this function, arboreal squirrels were well discriminated from scansorial and, especially, terrestrial species (Fig. 2). Arboreal squirrels along with *Plesiadapis* are characterized by high values of radial head shape (Tab. 10). In contrast, terres-

Tab. 6 - Median, lower and upper quartiles, and range of values of the calculated indices on radius.

	n	median	quartiles	range
	Radial Head Shape = (radial head width / radial head length) x 100			
Plesiadapis	2	80.32	--	6.43
Arboreal	4	84.52	80.39-86.75	10.34
Scansorial	5	81.58	80.49-82.00	9.06
Terrestrial	3	68.89	--	0.71
	Radial Head Depth = head depth / (head length x head width)			
Plesiadapis	2	2.09	--	0.72
Arboreal	4	2.34	1.84-3.08	1.60
Scansorial	5	2.93	2.52-2.98	1.18
Terrestrial	3	1.43	--	0.62

Tab. 7 - Median, lower and upper quartiles, and range of values of the calculated indices on femur.

	n	median	quartiles	range
Form of Distal Femoral End = (distal end height / biepicondylar width) x 100				
Plesiadapis	7	78.24	75.64-80.00	8.37
Arboreal	10	90.65	88.97-92.86	7.64
Scansorial	15	85.71	83.72-91.20	24.44
Terrestrial	8	97.46	94.56-106.94	24.43
Relative Form of Trochlea = (trochlea width / trochlea height) x 100				
Plesiadapis	6	69.98	63.37-73.47	22.14
Arboreal	10	65.32	59.05-68.09	22.63
Scansorial	15	61.29	56.00-63.33	24.31
Terrestrial	8	54.49	48.33-56.51	18.06

trial species are characterized by high values of femoral distal end shape and trochlear shape (Tab. 10). On the second function, arboreal squirrels were clearly discriminated from scansorial squirrels (Fig. 2). Along this function, arboreal species were once more characterized by high values of radial head shape, whereas scansorial squirrels were characterized by relatively high values of femoral distal end shape and trochlear shape (Tab. 10). It appears that radial head shape, femoral distal end shape, and femoral trochlear shape are the indices that are responsible for the best discriminantion of the three functional groups.

Discussion

The results of this study, of specific characters from selected postcranial elements of *Plesiadapis tricuspidens* and *P. n. sp.*, provide new data for the reconstruction of the locomotor and postural behavior of this Paleocene-Eocene plesiadapiform. In order to test the adaptive significance of the characters examined we used mammals that bear no phylogenetic relationship to the examined fossil, but are all part of a single phylogenetic group (i.e. the rodent family Sciuridae) that engage in different positional activities. Individual comparisons of selected indices placed *Plesiadapis* within arboreal squirrels. Furthermore, multivariate analyses (Principal Components and Discriminant Functions) provided similar results placing this Paleocene-Eocene mammal close to squirrels that habitually engage in quadrupedal walk and clamber on arboreal supports of different sizes as well as claw climbing on vertical supports.

Firstly, this suggests that P. tricuspidens was definitely an arboreal mammal, an assumption also supported by earlier studies (Szalay *et al*., 1975; Szalay & Dagosto, 1980; Jouffroy *et al*., 1991; Godinot & Beard, 1991). Secondly, this may imply that *Plesiadapis* most likely practiced to a large extent the same behaviors that are employed by these extant medium-sized squirrels. In this case, a comparative functional analysis of the postcranial elements that were presented in the previous section will help understand the range of local function and, consequently, the limb movements that can be associated with certain positional behaviors.

The relative length of the olecranon process distinguished well between arboreal and terrestrial squirrels. Arboreal forms were characterized by a relatively shorter olecranon compared to that of terrestrial runners and diggers. On the other

Tab. 8 - Median, lower and upper quartiles, and range of values of the calculated indices on the ungual phalanx.

	n	median	quartiles	range
Distal Wedging of Ungual Phalanx = (maximal height of ungual / ungual base height) x 100				
Plesiadapis	20	65.00	57.00-72.00	33.00
Arboreal	10	63.00	62.00-66.00	19.00
Scansorial	9	55.00	51.00-60.00	17.00
Terrestrial	7	49.00	48.00-50.00	12.00

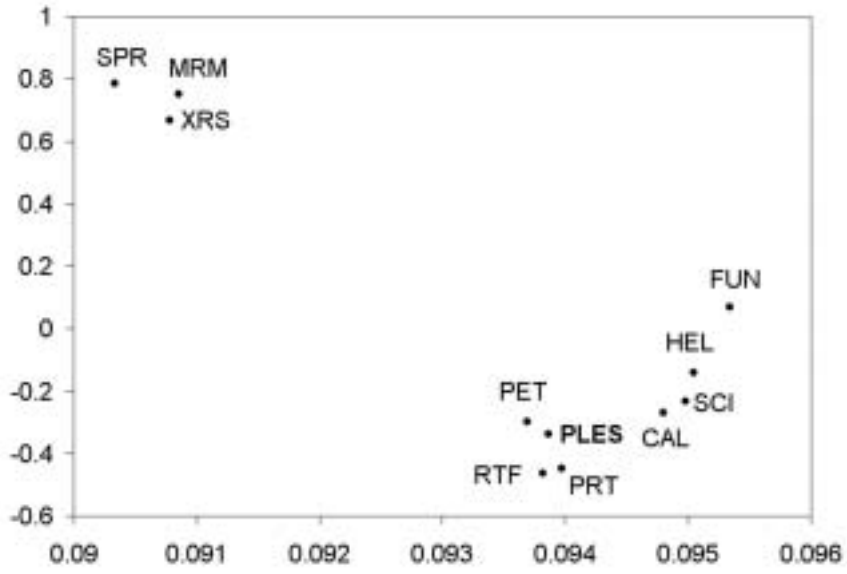


Fig. 1 - Plot of factors 1 and 2 of Principal Components Analysis of adjusted indices (divided by cube root of body weight). CAL: Callosciurus; FUN: Funambulus; HEL: Heliosciurus; MRM: Marmota; PET: Petaurista; PLES: Plesiadapis; PRT: Protoxerus; RTF: Ratufa; SCI: Sciurus; SPR: Spermophilus; XRS: Xerus.

Tab. 9 - Factor loadings of the adjusted indices, and eigenvalues and cumulative percentage of variance on the first 3 factors of the Principal Components Analysis.

	n	median	quartiles	range
Form of Distal Femoral End = (distal end height / biepicondylar width) x 100				
Plesiadapis	7	78.24	75.64-80.00	8.37
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Terrestrial	8	54.49	48.33-56.51	18.06

hand, *Plesiadapis* appeared to possess a moderately long olecranon (Szalay *et al*., 1975). This condition is also encountered in many arboreal marsupials, tupaiids, and arboreal quadrupedal primates (Richmond *et al*., 1998; Szalay & Sargis, 2001; Sargis, 2002c). The olecranon process is the insertion point for m. triceps brachii, the main forearm extensors, and a long olecranon would provide good leverage for powerful forearm extension (Hildebrand, 1995). On the other hand, a moderately long olecranon would suggest a less powerful extension of the forearm, and is most likely associated with frequently flexed arm postures (Schön Ybarra & Conroy, 1978; Szalay & Sargis, 2001; Sargis, 2002c). These forearm movements are necessary during arboreal walking and clambering when the center of gravity of the arboreal animal needs to be kept close to the support(s) (Cartmill, 1985). Moreover, arboreal mammals during walking and clambering on arboreal supports tend to adapt kinematically to the induced support reaction forces by maintaining flexed limb postures in order to reduce the applied bending loads (Schmitt, 1999).

The ulnar shaft of *Plesiadapis* was slightly robust (Szalay *et al*., 1975), hardly more robust than that of arboreal and scansorial squirrels but slenderer than that of terrestrial forms. The form of the ulnar shaft is associated with the presence and direction of bending forces that are applied to this bone during locomotor and postural behavior. A slightly robust shaft which is slightly narrow mediolaterally, is encountered in arboreal quadrupeds and should be related to reduced shear forces due to the low mediolateral support reaction forces that are applied during arboreal quadrupedal walk (Schmitt, 2003). In addition, a mediolaterally slender ulna would further indicate the presence of well-developed forearm muscles that favor a great range of pronation and supination, as well as powerful extensors and flexors of the hand and digits (Thorington *et al*., 1997), that facilitate forefoot accommodation on arboreal supports and powerful clinging capacities on vertical supports (Heinrich & Rose, 1997).

The roughly circular head of the radius that characterizes *Plesiadapis* appears to be a derived condition that is shared by Euprimates, but it is

not found in other early tertiary Eutheria (Szalay *et al*., 1975). Functionally, the shape of the radial head is related to the rotatory abilities of the forearm. Relatively round radial heads are also found in arboreal squirrels, primates, as well as arboreal tupaiids, and some arboreal marsupials and carnivorans (Taylor, 1974; Rose, 1988; Gebo & Sargis, 1994; Szalay & Sargis, 2001; Sargis, 2002c). This condition indicates a great extent of forearm supination and pronation and thus more mobility at the elbow joint as the radius rotates more freely on both humerus and ulna (Jenkins, 1973; Conroy, 1976; Rose, 1988; McLeod & Rose 1993; Szalay & Sargis, 2001). In *Plesiadapis*, this morphology is coupled with the well-excavated radial fossa that articulates with a humeral spheroidal capitulum (Szalay *et al*., 1975). This morphology is also shared by Euprimates, Plesiadapiformes, Dermoptera, Ptilocercus (but not tupaiines), but not Chiroptera (Beard, 1993; Sargis 2002). Other eutherians do not possess such well-excavated fossae, as was also demonstrated by the indices for arboreal squirrels. However, all arboreal forms bear relatively deeper fossae than terrestrial ones. This morphology promotes larger range of pronation-supination and high degree of humeroradial congruence throughout this range of movements (Conroy, 1976; Rose, 1988), as well as resistance to high loadings when the fore-

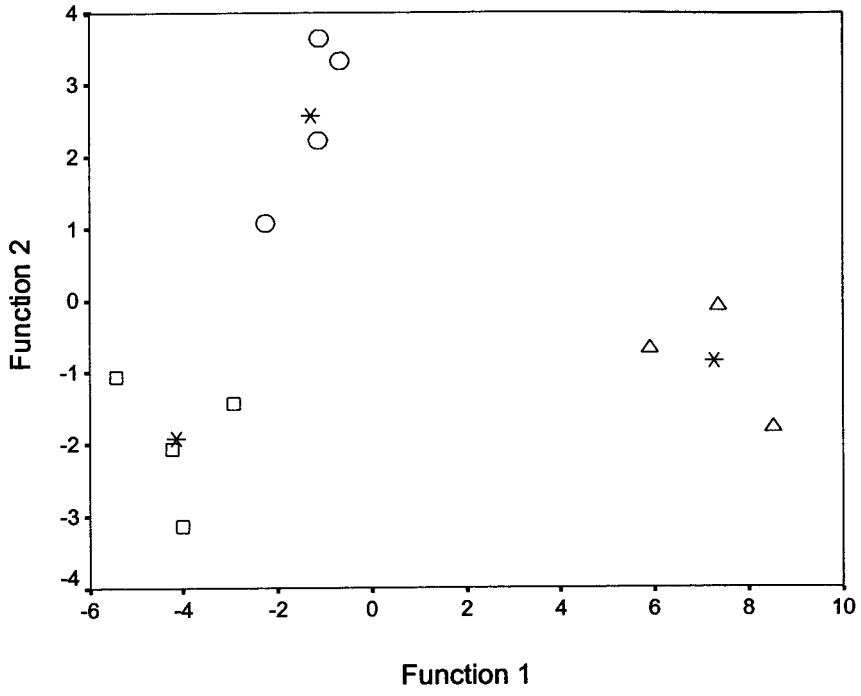


Fig. 2 - Discrimination of arboreal (including Plesiadapis) (squares), scansorial (circles), and terrestrial (triangles) squirrels based on their standardized canonical discriminant function coefficients depicted on functions 1 and 2 of the Discriminant Functions Analysis of adjusted indices (divided by cube root of body weight). The centroids for each functional group are represented by the asterisks.

Tab. 10 - Standardized canonical discriminant function coefficients of indices on functions 1 and 2 (a: variable that failed the tolerance criterium), locomotor group centroid values (b: arboreal squirrels comprise Plesiadapis), and eigenvalues and cumulative percentages of variance on functions 1 and 2 of the Discriminant Function Analysis.

	Function 1	Function 2
Olecranon height	1.232	-1.397
Ulnar form	-5.395	-5.361
Radial head shape	-21.382	-13.276
Radial head depth	0.976	3.267
Femur distal end shape	13.469	9.607
Femur trochlear shape	11.491	7.553
Ungual distal wedging [a]	--	--
Arboreal [b]	-4.154	-1.924
Scansorial	-1.290	2.568
Terrestrial	7.258	-.859
Eigenvalues	29.215	5.424
Cumulative %	84.3	100
Canonical correlation	0.983	0.919

arm is supinated during arboreal climbing and clinging activities (Beard, 1991). Moreover, this condition favors the transfer of load bearing from the humeroradial articulation to the humeroulnar articulation, freeing the radius for manipulative as well as more precise forearm postures necessary during all kinds of arboreal activities (Jenkins, 1973; Sargis, 2002c).

The distal femoral end of *Plesiadapis* is particularly wide and low, a condition that is considered primitive for Archontans and is shared by *Plesiadapisformes*, Dermoptera, Chiroptera, and Ptilocercus (Sargis, 2002d). A similar condition is encountered in lorisids, many arboreal marsupials, arboreal squirrels, and arboreal carnivorans that frequently employ arboreal deliberate quadrupedal walking and clambering as an important component of their positional behaviors (Tardieu, 1983; Ford, 1988; Anemone & Covert, 2000; Szalay & Sargis, 2001; Argot, 2002). The form of the distal femoral end is related to the leverage of m. quadriceps femoris, the main lower leg extensor. A high knee provides a better leverage for m. quadriceps femoris, increasing the mechanical advantage for rapid knee extension that is required for powerful propulsion during terrestrial cursorial activities (Tardieu, 1983; Ford, 1988). On the other hand, a low knee would favor less powerful but more controlled lower leg flexion and is indicative of

frequent flexed hind limb postures (Tardieu, 1983; Sargis, 2002). In addition, the wide morphology of the distal end would facilitate a less stabilized flexion and extension of the lower leg, which is associated with conjunct mediolateral movements that accommodate the frequent abductory and adductory hind limb movements on arboreal supports (Tardieu, 1983; Szalay & Sargis, 2001). These movements would favor deliberate quadrupedal walk and clamber on single or multiple arboreal supports.

The femoral trochlea in *Plesiadapis* was particularly low and wide, a character that is sometimes considered as an archontan or euarchontan apomorphy since it is shared by Plesiadapiformes, Dermoptera and Ptilocercus (Sargis, 2002b;d; contra Beard, 1993). The form of the femoral trochlea is frequently associated with the mobility or stability that occurs at the knee joint, that is the agility and not any support preferences (Argot, 2002). A wide and low trochlea is characteristic of arboreal primates, marsupials, and carnivorans that employ deliberate quadrupedal walk and/or frequent clambering and vertical climbing (Argot, 2002; Sargis, 2002d). This morphology promotes powerful flexion of the lower leg (Savage, 1957) allowing relatively ample mediolateral rotations of the tibia (Tardieu, 1983; Ford, 1988). Such hind limb movements are necessary during arboreal quadrupedal walk, climb, and clamber when the lower leg need to move freely and accommodate on the random position and direction of arboreal supports.

Plesiadapis was characterized by high and relatively short ungual phalanges that are also extremely compressed mediolaterally. This morphology is also shared by other Plesiadapiformes, Ptilocercus (not Tupaiines), Dermoptera and Chiroptera and is supposed to be a primitive Archontan character (Szalay & Lucas, 1996; Sargis, 2002b). Moreover, similar morphology is also encountered in highly arboreal squirrels and marsupial phalangerids (Beard, 1993; McLeod & Rose, 1993). High unguals imply a stout and robust morphology that can resist the bending forces that incur frequently during claw clinging and claw climbing on vertical or steeply inclined arboreal supports (Beard, 1991; Hamrick *et al*., 1999). Moreover, their relatively short length most likely provides an advantageous lever arm for powerful and precise control, which is necessary during all kinds of arboreal activities, and most particularly claw clinging and climbing (McLeod & Rose, 1993).

The combination of the characters of the ulna and radius suggested local functions that implied a frequently flexed elbow with certain mobility allowing a great range of pronation and supination maintaining extended humeroulnar and humeroradial contact. These functions are mainly associated with frequent deliberate arboreal quadrupedal walk and clamber on single or multiple horizontal and moderately inclined supports, as well as claw climbing and clinging on vertical or steep supports. Similarly, the morphology of the characters of the distal femoral end suggested a frequently flexed knee that is not stabilized, permitting ample mediolateral rotations of the lower leg. These functions are also associated with deliberate arboreal quadrupedal walk and clamber on single or multiple horizontal and moderately inclined supports. Lastly, the morphology of the ungual phalanges implies resistance to shear forces similar to those exerted during frequent claw climbing and clinging on vertical or steep supports. Thus, the studied postcranial characters suggest that P. tricuspidens was an arboreal mammal engaging primarily in deliberate quadrupedal activities such as walk and clamber on horizontal and moderately inclined supports, as well as claw climbing and clinging on more steeply inclined and vertical supports.

The fact that *Plesiadapis* is one of least specialized plesiadapiforms for its locomotion (Beard, 1991; 1993; Bloch & Boyer, 2002), and that the examined functional characters are also shared by other members of the Archonta (Beard, 1991; 1993; Szalay & Lucas, 1996; Bloch & Boyer, 2002), it is very likely that the positional morphotype of arboreal quadrupedal walk/clamber and claw climb/cling represents the ancestral archontan positional behavior. In this case, the different positional behaviors of other Eocene members of the cohort, should most likely represent derived conditions. In

regard to primates, it is hard to assess whether grasp-leaping (Szalay & Delson, 1979; Szalay & Dagosto, 1980; Dagosto, 1983; 1993; Szalay & Lucas 1996) or arboreal quadrupedalism and climbing (Godinot & Jouffroy, 1984; Ford, 1988; Godinot, 1991) best describe the ancestral morphotype locomotor behavior. If the arboreal quadrupedalwalking/clambering Plesiadapiformes are considered as close relatives to primates of modern aspect (Bloch & Silcox, 2001; Bloch & Boyer, 2002; Sargis, 2002a,b,c,d; Silcox, 2002) it is very likely that ancestral Euprimates might also have exhibited similar behaviors. On the other hand, if Tupaiidae, based on tarsal and other characters, is the sister group of Primates, then Ptilocercus would be closer to the ancestral primate locomotor mode. The fact that the early euprimate fossil record is still undersampled still leaves open debates (Rasmussen, 2002).

In any case, a reconstruction, as precise as possible, of the positional behavior of *Plesiadapis* appears important. The present study showed that both multivariate analyses as well as comparative functional morphology, placed *Plesiadapis* near the Asian giant squirrels Ratufa. Although, data on the positional behavior of this squirrel are limited, giant tree squirrels weigh around 2,200 gr., are mainly frugivorous and almost entirely arboreal, engaging in adept claw climbing on vertical trunks and supports as well as arboreal quadrupedalism upon slender branches in search of food sources (Nowak, 1991; Borges, 1998; Umapathy & Kumar, 2000). For these reasons, we believe that the best extant analog for the two species of *Plesiadapis* from the Paris Basin could be Ratufa. However, further research is required in order to document quantitatively and in detail the positional behavior of the different species of this Asian genus, as well as other similar sized tree squirrels.

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