

Ecomorphology of avian and nonavian theropod phalangeal proportions: Implications for the arboreal versus terrestrial origin of bird flight

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Abstract

The proportions of the nonungual phalanges of the hind foot, and the proportions of the hind limb bones, are used to interpret the locomotor habits of *Archaeopteryx* and other Mesozoic birds. In living birds with grasping feet, such as raptorial, perching, and trunk- and rock-clinging species, the penultimate phalanx of digits II, III and IV is characteristically longer than the more proximal phalanx. In primarily ground-dwelling birds, such as galliforms, gruiforms and ratites, the nonungual phalanges decrease in length proximodistally. Pedal and hind limb measurements were made on 191 Holocene birds to serve as a basis for comparison with hind foot and limb proportions in Mesozoic birds. Results were plotted on ternary diagrams and used in a principal components analysis. The clouds of points for primarily arboreal and terrestrial birds lie in separate but adjacent areas of ternary morphospace and are separated well on axes PC II and PC III. Within taxonomic groups (such as falconiforms, cuculiforms, hornbills and parrots), arboreal and terrestrial members fall in the appropriate clusters. Among Mesozoic birds, *Archaeopteryx* and *Confuciusornis* lie close to the junction between arboreal and terrestrial birds, in a region occupied by pigeons and galliforms, groups that forage both on the ground and in trees. *Iberomesornis* and *Sinornis* fall well within the arboreal cluster, and *Patagopteryx* and *Rahonavis* fall well within terrestrial birds. Analysis of manual phalangeal proportions in theropods, including *Archaeopteryx* and *Confuciusornis*, demonstrate a progressive increase in grasping specialization, with deinonychosaurs and the two birds being most specialized. Hind limb proportions show much overlap, but within groups relative length of the tarsometatarsus is a good indicator of relative arboreality or terrestriality. *Archaeopteryx* falls within the pigeon cluster, suggesting it is equally at home on the ground or in the trees.

Keywords

Locomotion, *Archaeopteryx*, Mesozoic birds, toes, fingers, hind limb.

Appendix 1: Comparison of phalangeal and hind limb proportions of living birds

Appendix 2: Results of principal components analysis of digits II and III

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Appendix 1: Comparison of phalangeal and hind limb proportions of living birds

The percent lengths of phalanges 1, 2 and 3 in pedal digit III and of hind limb bones in living species of birds that are primarily arboreal, trunk- or rock-clinging, and raptorial (Arb); primarily ground-walking or ground-running (Terr); or an uncertain combination of arboreal and terrestrial habits (Uncert).

	Habit	Pedal digit III			Femur	Tibia	Tarsusmetatarsus
		1	2	3			
Piciformes							
Picidae							
	All Arb						
<i>Colaptes auratus</i>		29.6	33.2	37.3	29.9	42.8	27.2
<i>Dryocopus lineatus</i>		25.7	31.4	42.9	32.2	40.3	27.5
<i>Dryocopus pileatus</i>		28.3	31.8	39.8	31.5	41.7	26.8
<i>Melanerpes erythrocephalus</i>		31.4	30.1	38.5	28.7	43	28.2
Rhamphastidae							
<i>Rhamphastos cuvieri</i>	Arb	31.9	32.9	35.2	28.3	44.5	27.2
Coliiformes							
Coliidae							
	All Arb						
<i>Urocolius macrourus</i>		24	33.3	42.7	29.9	43.2	26.8
<i>Colius striatus</i>		29.9	28	42.1	29.3	42.1	28.6
Coraciiformes							
Bucerotidae							
<i>Ceratogymna subcylindricus</i>	Arb	38.7	26.6	34.7	31.7	44.6	23.8
<i>Buceros rhinoceros</i>	Arb	40	28.5	31.5	32.3	44.4	23.3
<i>Anthracoceros coronatus</i>	Arb	38.1	28.1	33.9	31	43.6	25.4
<i>Tockus deckeni</i>	Uncert	38.6	29	32.4	28.7	42.8	28.5
<i>Tockus fasciatus</i>	Arb	39.5	27.8	32.8	30.2	44.5	25.4
<i>Bucorvus abyssinicus</i>	Terr	47	26	27	23.3	42.9	33.8
Alcedinidae							
	All Arb						
<i>Todirhamphus sanctus</i>		39.6	29.4	31	30.1	48.3	21.6
<i>Megaceryle torquata</i>		34.1	35	31	35.1	49	15.8
<i>Dacelo novaeguineae</i>		35.1	33	31.9	28.8	50.4	20.8
<i>Megaceryle alcyon</i>		37.6	28.8	33.6	31.5	54.6	13.9
<i>Alcedo cristata</i>		32.2	31.7	36.1	30.5	51.4	18.1
Coraciidae							
<i>Coracias</i> sp.	Arb	37.8	28.9	33.3	31.2	44	24.8
Meropidae							
<i>Merops viridis</i>	Arb	35.5	30.2	34.3	32.8	45.4	21.8
Brachypteraciidae							
<i>Brachypteracias leptosomus</i>	Uncert	35.3	31.4	33.2	27.2	42.9	30
Apodiformes							
Apodidae							
	All Arb						
<i>Chaetura cinereiventris</i>		18.8	21.2	60	29.5	46.8	23.8
Hemiprocnidae							
<i>Streptoprocne zonaris</i>	All Arb	30.3	20.3	49.4	29.7	46	24.3
Caprimulgiformes							
Steatornithidae							
<i>Steatornis caripensis</i>	Arb	34.8	27.6	37.5	35.4	46.3	18.3
Caprimulgidae							
<i>Caprimulgus carolinensis</i>	Terr	39.8	31.1	29.1	33.9	44.6	21.5
<i>Chordailes acutipennis</i>	Terr	42.5	32.6	24.9	31.9	46	22
Strigiformes							
Tytonidae							
	All Arb						
<i>Tyto alba</i>		23.1	36.7	40.2	25.2	43.9	30.9
<i>Tyto alba</i>		23.7	34.7	41.6	5.5	43.6	30.9

Continued.

Appendix 1, continued.

	Habit	Pedal digit III			Femur	Tibia	Tarsusmetatarsus
		1	2	3			
Strigidae							
	All Arb						
<i>Bubo virginianus</i>		25.1	26.4	48.6	30.5	45.9	23.6
<i>Bubo virginianus</i>		27.3	26	46.8	30.9	46	23.1
<i>Bubo virginianus</i>		25.6	25.5	48.9	30.7	45.4	24
<i>Strix varia</i>		22.9	30.5	46.7	31.6	45	23.4
<i>Otus atricapillus</i>		23.2	30.1	46.8	30.7	45.3	24
<i>Speotyto cunicularia</i>		25.2	31	43.8	26.4	43.3	30.3
Cuculiformes							
Musophagidae							
	All Arb						
<i>Tauraco hartlaubi</i>		37.1	31.5	31.4	31.3	43.8	25
<i>Tauraco macrorhynchus</i>		37.1	32.4	30.5	31.8	43.6	24.5
<i>Musophaga violacea</i>		36.5	30.7	32.8	31.1	44	24.8
<i>Tauraco corythaix</i>		36.7	31.1	32.2	30.9	43.9	25.2
<i>Corythaixoides concolor</i>		37.9	32.6	29.5	31.1	44.9	24
Opisthocomidae							
<i>Opisthocomus hoazin</i>	Arb	33.7	33.9	32.4	30.8	42.5	26.7
Cuculidae							
<i>Coccyzus erythrophthalmus</i>	Arb	31.3	31.2	37.6	30.8	42.2	27
<i>Coccyzus americana</i>	Arb	35.7	29	35.3	29.4	43.2	27.4
<i>Cuculus fugax</i>	Arb	36.2	31.3	32.5	30.4	43.7	25.9
<i>Crotophaga ani</i>	Terr	37.1	30.9	32	25.3	44.2	30.5
<i>Guira guira</i>	Terr	36.5	30	33.4	27.3	43.3	29.4
<i>Coua serriana</i>	Terr	39.2	31.5	29.3	26.3	42.1	31.6
<i>Eudynamys scolopacea</i>	Arb	36.7	30.1	33.2	29.6	42.8	27.6
<i>Geococcyx californianus</i>	Terr	38	33.6	28.4	26.9	42.1	31
<i>Geococcyx californianus</i>	Terr	37.9	34.2	28	27.1	41.4	31.5
<i>Centropus sengalensis</i>	Terr	37.5	33	29.5	29.6	42	28.4
Psittaciformes							
Psittacidae							
<i>Ara severa</i>	Arb	33.8	26.8	39.4	34.6	48.4	17
<i>Cacatua ducorpsii</i>	Arb	35.3	28.1	36.6	33.7	50.2	16.1
<i>Nestor notabilis</i>	Arb	35.1	27.6	37.3	30.6	46.9	22.5
<i>Nestor notabilis</i>	Arb	36.2	28.8	35.1	30.5	47.7	21.8
<i>Nestor meridionalis</i>	Arb	35	25.1	39.9	29.8	48.9	21.3
<i>Aratinga leucophthalmus</i>	Arb	35.1	26.7	38.2	34.5	47.6	17.9
<i>Aratinga leucophthalmus</i>	Arb	31.8	27.4	40.7	34.3	47.7	17.9
<i>Strigops habroptilus</i>	Terr	37.7	31.1	31.3	32.8	46.1	21.1
<i>Cacatua leadbeateri</i>	Arb	33.8	27.4	38.8	33.4	50.2	16.3
<i>Anodorhynchus hyacinthinus</i>	Arb	32.6	27	40.4	34.2	47.6	18.2
<i>Psittacus erithacus</i>	Arb	33.5	27.4	39.1	35.1	48.2	16.7
<i>Probosciger aterrimus</i>	Arb	37.6	28.4	34.1	33.8	50.4	15.8
Columbiformes							
Columbidae							
<i>Columba livia</i>	Terr	40.8	31.9	27.3	30.9	45.1	24
<i>Columba livia</i>	Terr	41.3	31.2	27.5	30.9	44.6	24.5
<i>Columba palumbus</i>	Arb	37.9	32	30.1	32.5	43.9	23.6
<i>Columba fasciata</i>	Uncert	37.6	32.1	30.3	32.4	44.1	23.5
<i>Columba leucocephala</i>	Arb	36.4	32.8	30.7	32.2	43.9	23.9
<i>Zenaida macroura</i>	Terr	37.8	32.5	29.8	31.8	43.6	24.6
<i>Zenaida galapagoensis</i>	Terr	39.2	32.4	28.5	29.5	45	25.5
<i>Treron australis</i>	Arb	37.1	33	29.9	34.2	43.8	22
<i>Caloenas nicobarica</i>	Terr	40.4	30.4	29.2	29.2	44.1	26.7
<i>Ptilinopus jambu</i>	Arb	35.8	32.4	31.8	33.1	43.6	23.3
<i>Goura cristata</i>	Terr	42.6	30.5	27	27	42.5	30.5
<i>Leptoptila verreauxi</i>	Terr	39.6	30.9	29.5	29.8	43.7	26.4
<i>Phaps calcoptera</i>	Terr	42.9	29.2	27.9	32.1	44.6	23.3
<i>Geotrygon montana</i>	Terr	39.2	33	27.9	29.5	43.3	27.2

Continued.

Appendix 1, continued.

	Habit	Pedal digit III			Femur	Tibia	Tarsusmetatarsus
		1	2	3			
<i>Gallicolumba jobiensis</i>	Terr	40.1	31.4	28.5	30	43.4	26.7
<i>Didunculus strigirostris</i>	Uncert	40.2	29.9	29.9	30.9	43.1	26
<i>Geophaps lophotes</i>	Terr	39.2	31.2	29.7	31.8	43.4	24.7
Raphidae							
<i>Raphus cucullatus</i>	Terr	46.1	30.7	23.2	32.7	45.2	22.1
Pteroclididae	All Terr						
<i>Syrhaptus paradoxus</i>		50.1	29.2	20.7	34.6	46.1	19.3
<i>Pterocles alchata</i>		49.4	30.4	20.2	34.2	45.9	19.9
<i>Pterocles quadricinctus</i>		46.4	32.6	21	33.3	42.5	24.2
Charadriiformes							
Glareolidae	All Terr						
<i>Pluvialis squatarola</i>		43	31.9	25.1	23	45.3	31.7
<i>Glareola pratincola</i>		41.9	30.3	27.8	24.7	43.5	31.8
Burhinidae	All Terr						
<i>Burhinus magnirostris</i>		42.6	33.3	24.1	17.9	43.3	38.8
Scalopaciidae	All Terr						
<i>Scalopax minor</i>		41.7	31.2	27.1	29.9	43.4	26.6
Jacaniidae	All Terr						
<i>Jacana spinosa</i>		45.5	30.8	23.6	17.9	47.2	34.9
Gruiformes							
Gruidae	All Terr						
<i>Grus japonensis</i>		45.8	29.6	24.6	18.8	43.9	37.3
<i>Balearica pavonina</i>		40.7	31	28.3	17.6	47.9	34.5
Rallidae	All Terr						
<i>Gallinula chloropus</i>		39.1	30.6	30.3	26.5	44.2	29.3
Cariamidae	All Terr						
<i>Cariama cristata</i>		48.7	30.2	21.1	20.3	43	36.7
Psophiidae	All Terr						
<i>Psophia leucoptera</i>		39.2	29.2	31.6	20.8	43.6	35.6
Otididae	All Terr						
<i>Otis tarda</i>		53.7	30.7	15.6	24	43.8	32.2
Turnicidae	All Terr						
<i>Turnix varia</i>		45.3	28.6	26.1	33.6	42.1	24.3
<i>Turnix sylvatica</i>		45.3	28.6	26.1	31.9	42.3	25.8
Galliformes							
Numididae	All Terr						
<i>Numida meleagris</i>		42.6	31.9	25.6	26.2	40.6	33.1
<i>Acryllium vulturinum</i>		42.4	30.9	26.8	26.4	42.7	30.9
Phasianidae	All Terr						
<i>Meleagris gallopavo</i>		39.4	34	26.5	25.2	43.8	31
<i>Pavo cristatus</i>		40.3	31.5	28.2	25.5	44.6	29.9
<i>Gallus gallus</i>		41.2	31.5	27.2	29.5	41.9	28.6
<i>Gallus gallus</i>		41.1	30.1	28.8	29.8	41.3	28.9
<i>Colinus virginiana</i>		39.2	31.6	29.2	33.4	42.7	23.9
<i>Cyrtornis montezumae</i>		39.4	28.9	31.6	33.5	42.5	24
<i>Alectornis chukar</i>		39.7	32.1	28.2	32.2	42.9	24.9
<i>Lophophorus impejanus</i>		36.7	33	30.3	31.9	42.8	25.3
Megapodiidae	All Terr						
<i>Leipoa ocellata</i>		46.7	29.6	23.8	29.5	43.7	26.8
<i>Macrocephalon maleo</i>		48.7	28.5	22.8	28.1	41.9	30
Cracidae	All Arb						
<i>Crax globulosa</i>		43	32.5	24.4	29.3	42.6	28.1
<i>Penelope jacquacu</i>		39.7	32.1	28.2	29.9	42.4	27.6
<i>Ortalis motmot</i>		39.1	32.6	28.3	29.2	43	27.8
<i>Ortalis vetula</i>		40.1	32.1	27.8	28.7	44.1	27.2
<i>Aburria aburri</i>		38.3	31.8	29.9	30.9	43.4	25.7
<i>Pipile cumanensis</i>		38.3	32.5	29.2	30.8	43.6	25.6

Continued.

Appendix 1, continued.

	Habit	Pedal digit III			Femur	Tibia	Tarsusmetatarsus
		1	2	3			
Falconiformes							
Cathartidae							
	All Terr						
<i>Sarcorhamphus papa</i>		37.5	31.4	31.1	27.3	45.5	27.2
<i>Coragyps atratus</i>		39.4	32.7	27.9	27.9	45.8	26.3
<i>Cathartes aura</i>		38.1	31.8	30.2	27.7	46	26.3
Falconidae							
<i>Phalcobaenus megalopterus</i>	Terr	44.5	27.2	28.2	27.1	39.5	33.4
<i>Daptrius ater</i>	Terr	39.7	29.6	30.7	27	41.6	31.4
<i>Polyborus plancus</i>	Terr	44.7	26.8	28.4	25.4	41.3	33.3
<i>Polyborus plancus</i>	Terr	44.2	27.7	28.1	23.7	41.6	34.7
<i>Falco sparverius</i>	Arb	40.3	27.1	32.6	29.7	40.6	29.8
<i>Falco peregrinus</i>	Arb	40.1	27.4	32.5	32.8	42.2	24.9
Sagittariidae							
<i>Sagittarius serpentarius</i>	Terr	51.3	26.2	22.5	15.8	42.5	41.7
<i>Sagittarius serpentarius</i>	Terr	51.9	25.7	22.4	15.1	43	42
Pandionidae							
<i>Pandion haliaetus</i>	Arb	34.9	12.9	52.2	29.4	49.7	20.9
<i>Pandion haliaetus</i>	Arb	36	14	50	29.7	49.2	21.1
Accipitridae							
<i>Gyps fulvus</i>	Terr	41.1	31.4	27.6	31	43.7	25.3
<i>Necocertes monachus</i>	Terr	42.2	30	27.8	28.7	43.6	27.7
<i>Morphnus guianensis</i>	Arb	41.4	18.9	39.7	27.2	42.7	30.1
<i>Ictinia mississippiensis</i>	Arb	38.5	27.2	34.3	31.5	43.1	25.5
<i>Haliaeetus leucocephalus</i>	Arb	43.7	20.8	35.5	31.5	43	25.5
<i>Circus cyaneus</i>	Arb	45	19.1	35.9	27.7	40.3	31.9
<i>Circus cyaneus</i>	Arb	44.8	18.1	37.1	27.7	40.6	31.7
<i>Buteo jamaicensis</i>	Arb	42.6	17.6	39.9	30.5	39.8	29.7
<i>Buteo jamaicensis</i>	Arb	42.6	18.4	39	29.7	40.1	30.2
<i>Aquila chrysaetos</i>	Arb	43.9	17.8	38.4	1.2	42.2	26.5
<i>Circaetus gallicus</i>	Arb	40.7	17.9	41.4	26.5	42	31.5
Anseriformes							
Anhimidae							
<i>Anhima cornuta</i>	Terr	38.7	34.1	27.3	23.9	45	31.1
Ciconiiformes							
Ciconiidae							
<i>Leptoptilos crumeniferus</i>	All Terr	49	30.1	20.8	16.6	47	36.4
Ardeidae							
<i>Botaurus lentiginosus</i>	All Terr	36.5	36.2	27.3	26.7	43.4	29.9
Tinamiformes							
Tinamidae							
<i>Tinamus major</i>	All Terr	44.2	33.1	22.7	29.5	42.4	28.1
<i>Crypturellus soui</i>		41.9	33	25.1	30.6	43	26.4
Apterygiformes							
Apterygidae							
<i>Apteryx australis</i>	All Terr	43.5	30.4	26.1	31	45.1	24
<i>Apteryx australis</i>		41.4	30	28.7	30.8	44.4	24.8
Casuariiformes							
Casuariidae							
<i>Casuarus unappendiculatus</i>	All Terr	46.9	32.4	20.8	25.8	41.5	32.7
Dromaiidae							
<i>Dromaius novaehollandiae</i>	All Terr	50	31.5	18.5	21.9	40.3	37.7
Rheiformes							
Rheidae							
<i>Rhea americana</i>	All Terr	52.6	32.2	15.3	24.9	38.1	37
<i>Pterocnemia pennata</i>		48.4	34.2	17.4	25.9	37.9	36.2

Continued.

Appendix 1, continued.

	Habit	Pedal digit III			Femur	Tibia	Tarsusmetatarsus
		1	2	3			
Struthioniformes							
Struthiidae							
<i>Struthio camelus</i>	Terr	51.9	30.2	17.9	23.2	41	35.8
Passeriformes							
Dendrocolaptidae							
<i>Deconychura longicauda</i>	All Arb	25.8	31	43.2	27.2	39.3	33.5
<i>Dendrocolaptes certhia</i>		30.6	30.3	39.1	29.2	38.2	32.5
Furnariidae							
<i>Furnarius rufus</i>	Terr	35	31.9	33	24.7	42.7	32.6
Formicariidae							
<i>Myrmeciza hyperythra</i>	Arb	32.1	30.6	37.3	25.5	41.4	33.1
Rhinocryptidae							
<i>Scelorchilus rubecula</i>	Terr	37.4	34.1	28.5	23.4	43	33.6
Tyrannidae							
<i>Tyrannus melancholicus</i>	Arb	32.1	28.3	39.5	28.5	43.5	28
<i>Empidonax trailii</i>	Arb	27.6	25.3	47.1	24.7	44	31.3
Pittidae							
<i>Pitta mackloti</i>	Terr	32.1	34.6	33.3	24.4	42.2	33.4
Menuridae							
<i>Menura novaehollandiae</i>	Terr	27.6	33.2	39.2	21.6	42.5	35.9
Alaudidae							
<i>Melanocorypha mongolica</i>	Terr	41.1	31.5	27.4	28.1	42.2	29.7
Hirundinidae							
<i>Riparia riparia</i>	Arb	35.8	25.8	38.4	29.1	46.6	24.3
Motacillidae							
<i>Motacilla aguimp</i>	Terr	36.2	32.2	31.6	23.5	43.7	32.8
Cinclidae							
<i>Cinclus cinclus</i>	Terr	34.5	35	30.5	23.5	44.7	31.8
Troglodytidae							
<i>Cistothorus platensis</i>	Arb	29.2	34.7	36.1	25.8	43.7	30.5
Mimidae							
<i>Mimus polyglottos</i>	Arb	33.3	32.2	34.5	23.6	43.6	32.8
<i>Toxostoma rufum</i>	Arb	36.5	32.2	31.3	24.5	44	31.5
Muscicapidae							
<i>Catharus fuscescens</i>	Arb	31	30.9	38	23.1	44.1	32.8
Paridae							
<i>Parus atricapillus</i>	Arb	33.3	25.6	41	24.4	44.5	31.1
Sittidae							
<i>Sitta castanea</i>	Arb	30.4	33.2	36.4	26.6	42	31.4
Certhiidae							
<i>Certhia familiaris</i>	Arb	31.7	31.5	36.9	24.8	41	34.2
Icteridae							
<i>Quiscalus quiscula</i>	Uncert	33.9	32.1	34	26.7	42.5	30.8
<i>Gymnostinops bifasciatus</i>	Arb	31.9	29.6	38.5	32.3	52.5	15.1
<i>Sturnella neglecta</i>	Terr	33.7	35.3	31	26.2	42	31.8
Sturnidae							
<i>Cosmopsarus regius</i>	Uncert	33	33.1	34	25.7	42.9	31.4
<i>Sturnus vulgaris</i>	Terr	34.7	31.8	33.6	26.9	44.6	28.5
Grallinidae							
<i>Grallina cyanoleuca</i>	Terr	34.3	31.1	34.5	22.5	43.1	34.4
Corcoracidae							
<i>Corcorax melanorhamphus</i>	Terr	34.9	32	33.1	23.7	43.6	32.7
Artamidae							
<i>Pityriasis gymnocephala</i>	Arb	28.8	28.5	42.6	29.6	41.9	28.4
Cracticidae							
<i>Gymnorhina tibicen</i>	Terr	34	33.6	32.4	23.8	44.7	31.5
<i>Gymnorhina tibicen</i>	Terr	31.2	32.8	36	24.5	44.2	31.3
<i>Strepera graculina</i>	Terr	29.5	33.9	36.7	25.8	44.2	30
<i>Cracticus nigrogularis</i>	Arb	29.8	32.1	38.2	27.1	43.5	29.4

Continued.

Appendix 1, continued.

	Habit	Pedal digit III			Femur	Tibia	Tarsusmetatarsus
		1	2	3			
<i>Cracticus torquatus</i>	Arb	28.2	33.8	38	28.2	42.6	29.2
Ptilonorhynchidae							
<i>Chlamydera maculata</i>	Terr	30.6	33.6	35.8	26.1	44.3	29.6
Corvidae	All Arb						
<i>Pica pica</i>		34.1	31.5	34.4	25	43.6	31.4
<i>Corvus corax</i>		32.2	31.3	36.5	27.8	46	26.2
<i>Corvus brachyrhynchus</i>		33.7	31.2	35.1	26.4	44.3	29.3
<i>Cyanositta cristata</i>		31.1	28.7	40.2	26.6	42.5	30.8
<i>Cyanositta cristata</i>		29.4	32	38.6	26.5	42.4	31.1

Appendix 2: Results of principal components analysis of digits II and III

Component loadings

	1	2	3	4	5
A	0.608	0.091	-0.150	0.001	0.007
B	0.533	0.079	0.055	-0.103	-0.031
C	0.454	-0.200	0.021	-0.031	0.062
D	0.597	0.158	0.086	0.074	0.019
E	0.498	-0.204	0.001	0.048	-0.055

Variance explained by components (Eigenvalues)

	1	2	3	4	5
	1.464	0.121	0.033	0.019	0.008

Percent of total variance explained

	1	2	3	4	5
	88.953	7.341	2.032	1.176	0.497