

Theoretical morphology of the Archosaur (Reptilia: Diapsida) pelvic girdle

Diego Rasskin-Gutman and Angela D. Buscalioni

Abstract.—Theoretical models of skeletal structures provide suitable frameworks to assess macro-evolutionary patterns of form change. We discuss three theoretical approaches to account for morphological patterns of the pelvic girdle in archosaurs. Every approach targets a different level of organization within the concept of morphospace. First, we build a morphocline by applying a mathematical transformation to the outline of the hip of the theropod dinosaur *Deinonychus antirrhopus*, in order to look at theoretical paths of evolutionary change based on changes of proportion. Second, we analyze the variability of a sample of 86 hips within a theoretical construction that incorporates information about the spatial orientation of the three paired bones that build this skeletal compound. Finally, we look at boundary patterns within these hips as a basis for generating a formalism based on graph theory. Insights about the evolution and development of the archosaur triradiate pelvis and its morphological trends are suggested in the light of each theoretical approach, with a special focus on the convergent evolution of a retroverted pubis in ornithischians and birds.

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Introduction

The analysis of organic form has a central place in the development of comparative methods to understand life histories, phylogenetic relations among different taxa, and evolutionary processes. Model making and abstractions are useful approaches to generate comparative formal frameworks because of their generality. Furthermore, the use of model-making methodologies prompts an exploration of common underlying causes for the patterns and processes these models represent. Many authors have advocated the use of theoretical models in biology, pointing out the potential gain that a theoretical perspective can offer when trying to explain biological systems (e.g., Thompson [1917] 1942; Lotka [1924] 1956; Woodger 1937; Rashevsky 1944; Sommerhoff 1950; and, more recently, Goodwin 1963; Waddington 1968; Thom [1972] 1977; Mandelbrot 1983; Gould 1991; and Rosen 1991).

Theoretical morphology and its operative vehicle, morphospace, offer a set of unique features to build comparative frameworks in order to understand morphological organi-

zation (see Chapman and Rasskin-Gutman 1999; and for a recent introduction to theoretical morphology methodologies, McGhee 1999). The contrast of the “possible” against the empirically “observable” poses questions about the logic of the observable, about those organizations that are “impossible,” as well as about those organizations that, although possible, have never been explored by natural evolution. The abstraction of systems by a few variables represents a shortcoming of this approach that, nevertheless, helps in the search for “hidden variables” (variables that have not been abstracted in the model) (see Wimsatt 1987), enabling a new interpretation of the modeled system itself. For example, Rosas (1992) offered insights on the morphological traits of the hominid mandible by recognizing the development of the frontal lobules of the brain during embryonic growth as a hidden variable that modifies the flexion of the skull. Also, Alberch and Gale (1985) gave a possible explanation for the tendency to lose digits in miniature amphibians (frogs and salamanders), using a morphogenetic model of the appendicular skeleton in vertebrates rather than

a traditional explanation based on selective forces.

This paper derives insights on morphological constraints, covariations, and macroevolutionary patterns in the pelvic girdle of archosaur groups using theoretical morphology methodologies. The search for a hidden variable will prompt us to propose a hypothesis in which a developmental mechanism is responsible for the convergence of pubic orientations in archosaur hips. Three levels of abstraction will be explored. The first level involves the analysis of morphological transformations from the outline of the lateral view of a theropod dinosaur pelvis in order to explore a possible morphocline in the origin of Aves. The second level involves the analysis of the relative spatial arrangement of each hip bone. Finally, the third level searches for a formalism to describe the boundary patterns of the pelvis as a skeletal compound in archosaur forms.

The Pelvic Girdle in Archosaurs

The pelvic girdle is conservative in its overall morphological organization. The dorsal ilium contacts the sacral vertebrae through its medial surface, providing a connection point between the vertebral column and the hindlimbs. It also provides attachment sites for thigh muscles connecting to the femur, tibia and fibula (e.g., *Mm. iliofemoralis*, *iliotibialis*, and *iliofibularis*). The ventral elements, pubis and ischium, also provide attachment sites for muscles that move the leg (e.g., *Mm. puboischiofemorales externus*). The pubis, which occupies an anterior position in relation to the ischium, is related to cranial structures of the postcranial skeleton in most groups. Thus, the attachment of *M. rectus abdominis* (accompanied in some groups by dermal bones called *gastralia*) to the distal pubis is involved in protection and support of most abdominal organs. This connection is assumed to provide a tensile force that strains the bowl-like structure of the vertebral column by joining the sternal plates to the pubes. On the other hand, the ischium is related to the caudal structures of the organism, in particular to the cloacal system. In archosaurs, a characteristic modification of the ventral elements took place. Instead of re-

taining a platelike pubis and ischium, an opening (the puboischadic fenestra) between both bones appeared; also, both bones became elongated into an arrangement called the tri-radiate pelvis (Romer 1956). Different pubic orientations traditionally defined two groups of archosaurs: the propubic (anteriorly oriented pubis) and the opisthopubic (posteriorly oriented pubis). A third category should be added, the mesopubic, with a vertically oriented pubis, to better describe this continuum (Rasskin-Gutman 1997). The pubis is highly variable: it may be fused to the ischium (e.g., pterosaurs), it may practically disappear (e.g., ankylosaurs), it may diminish (e.g., Aves), it may lose its iliac contact, so that it connects through an extra cartilaginous element (e.g., the *pars acetabularis* in crocodiles [Goodrich 1986]), or otherwise, it may be a prominent element in the pelvic girdle (e.g., non-avian theropods).

As a functional complex, the pelvis supports and transmits the weight of the individual, acts as a point of anchorage for the hindlimbs (including muscle attachment surfaces), interacting with the lumbar, sacral, and caudal regions of the vertebral column. It has a protection role for different organs, e.g., digestive, ventilatory, and urogenital systems, sometimes acting as a protective dome for essential organs such as the kidneys in birds. The pelvis is a dynamic structure in some groups, such as crocodiles, in which the pubes are directly related to diaphragmatic movements during ventilation. All of these aspects confer on the pelvis a dual static (support, protection) and dynamic (locomotion, articulation, ventilation) functionality, which is used in varying ways by different groups.

The Archosauriformes clade was defined by Gauthier et al. (1988). As a lineage, the Archosauriformes represents a good example of a group that has diversified in many habitats, with different locomotor patterns associated with specific sets of morphological characters: terrestrial quadrupeds (sauropods, crocodiles, etc.); terrestrial bipeds (theropods); flyers (pterosaurs, birds); and swimmers (marine crocodiles). Each group, in turn, has a number of different stance and gait patterns (see, for example, Parrish 1986; Alexander 1989; Sereno

TABLE 1. Levels of morphological organization. In a vertebrate skeleton elements are bones (e.g., the ilium); compounds are spatial associations of bones with physical borders (e.g., the pelvis); and mechanisms are dynamical associations of elements and compounds, which can move to different spatial conformations (e.g., the pelvis plus the hindlimb).

Organizational level	Descriptor	Formalization	Morphospace
Proportions	Element	Character matrix	Hyperspace
Orientations	Compound	Angles, positions	Dispospace
Connections	Compound	Boundary patterns	Connectivity space
Articulations	Mechanism	Angles, distances	Conformation space

1991a; Gatesy 1995; Gatesy and Dial 1996). Considering these broad differences in locomotory patterns, and over more than 250 m.y. of evolutionary history, we might expect a wide range of variation in the number of elements with different connections between them, as has occurred with other structures such as the limbs (Shubin and Alberch 1986). Instead, the pelvic girdle has been almost invariably built with three paired bones showing the same connections between them, with the central acetabulum as a supporting cavity for the hindlimbs. However, there are obvious differences among taxa in proportions, ranges of orientations (especially for the pubis), as well as different connections between bones, which offers a good opportunity to conduct an analysis using theoretical morphology.

Following the anatomical tradition (ever since Cuvier) of identifying form with function, most studies on archosaur hips have been centered on the role of the pelvic bones as attachment surfaces for locomotor muscles (e.g., Romer 1923; Galton 1969; Charig 1972; Walker 1977; Parrish 1986; Rowe 1986). As a result, the pelvis has mostly been explained by alluding to some functional locomotor requirement, e.g., sprawled versus upright stance, quadrupedal versus bipedal gait. However, each archosaur lineage presents a variety of non-unique architectural hip types, which results in the presence of several convergent features. A persistent focus on the pelvis as a locomotor “accessory” has undoubtedly yielded a good understanding of the role of the muscles involved in hindlimb and tail movement (e.g., Gatesy 1997), yet basic questions about the evolution of the pelvis morphology remain unanswered, such as the convergence

of a retroverted pubis in ornithischians and birds.

Materials and Methods

As a general, encompassing framework to analyze form, we identify four levels of morphological organization (Table 1): proportions (described by elements), orientations and connections (described by compounds), and articulations (described by mechanisms). Each level of organization is characterized by a set of specific properties, formalized in a different way, and analyzed in the context of a different morphospace. The isolated bone (an element) is described in terms of proportions (size and shape). A character matrix formalizes elements, and the morphospace is built as a multidimensional character space (hyperspace of coordinates, lengths, discrete features, etc., as commonly used in morphometrics). Compounds are spatially associated bones that form borders, establishing connectivity relations. Borders give cohesion to the elements of a compound, setting the stability of their spatial disposition. Two levels of description can be identified for a compound: orientations and connections. The spatial orientations are formalized by means of a multidimensional matrix of angles and distances inside a morphospace construction that represents a space of orientations or “dispospace.” Connections are best described as boundary patterns, defined as contact between bones. The incidence or adjacency matrix is an adequate formal tool for connectivity relations, and the morphospace is the space of connections. Finally, mechanisms describe the level of articulation. A mechanism is a set of elements (or compounds, or both) in which one element is ca-

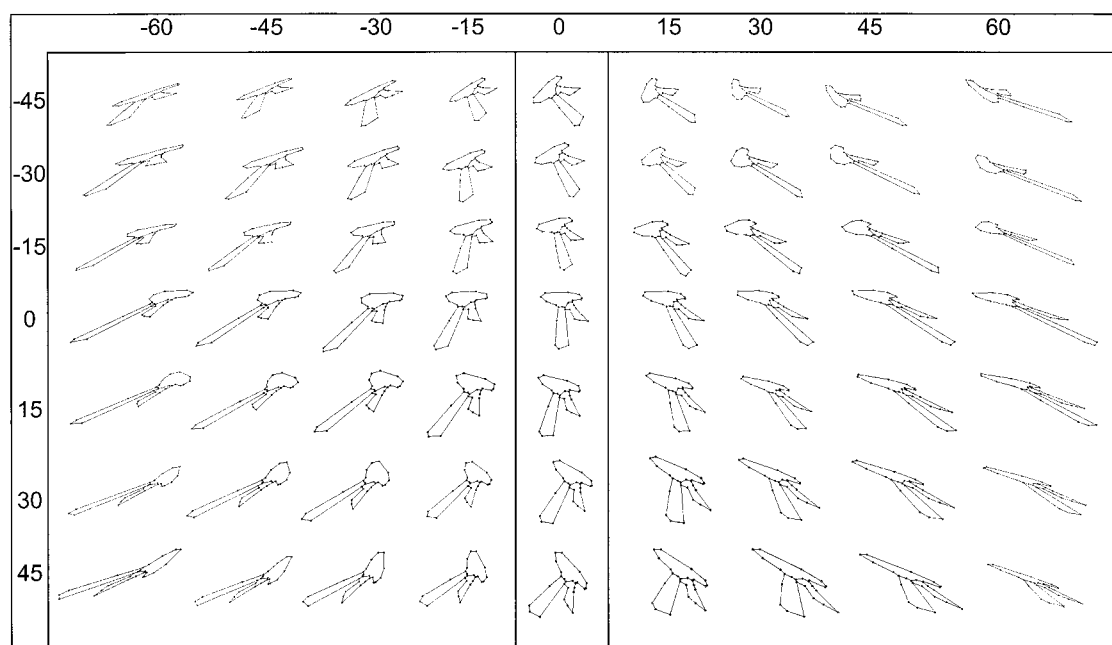


FIGURE 1. Affine morphospace of the hip outline of the theropod dinosaur *Deinonychus antirrhopus* abstracted with 25 landmarks. A uniform transformation function was applied to the outlines highlighted in the center. Parameter ANG, horizontal axis, controls the extent and direction of the strain; ROT, vertical axis, in degrees, controls the rotation from the initial, vertical position in the center of the morphospace. Note that features such as the pubic foot seem distorted (see Rasskin-Gutman and Buscalioni 1996 for a more detailed account of the morphocline construction).

pable of reaching different positions (e.g., the pelvis associated with the hindlimb). In contrast with compounds, which are static, mechanisms are dynamic, showing mobility. A morphospace of conformations (mainly angles and distances) is a suitable framework for mechanisms. Since the pelvis is a static compound, we center our analysis on the proportions, orientations, and connections of its bones.

Proportions: The Affine Morphospace.—Proportions of the pelvic morphology are studied with a model of the shape of the outline of the hip in terms of bidimensional coordinates. The lateral contour of the pelvic girdle of *Deinonychus antirrhopus* was digitized as a collection of 25 landmarks (Fig. 1) from the drawing of Ostrom (1976). Using the computer program D'ARCYGRAPH (Rasskin-Gutman 1995; Rasskin-Gutman and Buscalioni 1996), several uniform models of change were applied to this outline, generating morphoclines. After each application of the uniform function, the transformed coordinates of the original out-

line were saved. Together, the collection of different theoretical morphoclines forms an "affine morphospace" (affine transformations are uniform transformations that keep parallelism between lines) (see Rasskin-Gutman and Buscalioni 1996 for a more detailed explanation of this procedure). Diagrams of 13 archosaurs were digitized by using the same 25 landmarks (see Table 2 for sources). These are: *Proterosuchus*, *Anhanguera*, *Herrerasaurus*, *Avimimus*, *Compsognathus*, *Gallimimus*, *Allosaurus*, *Archaeopteryx*, *Gallus*, *Riojasaurus*, *Lesothosaurus*, *Hypsilophodon*, and *Kritosaurus*. The simulations of the morphocline that approximates both the retroversion and the anteroversion of the pubis from the initial conditions provided by the coordinates of *Deinonychus* were selected and used along with the coordinates of these real hips to generate a minimum spanning tree using the statistical package NTSYSPC version 1.80. The tree was built using euclidean phenetic distances, calculated previously with a shape analysis superimposition procedure in which the baseline was chosen as

TABLE 2. List of taxa showing chronological ranges of their record, orientation type, boundary pattern, and locomotory pattern for each genus. Refer to the dispace and the connection space for orientation and boundary pattern numbers. ilp = projection of the ilium ((d1/d1+d2)*100); pa = public angle, in degrees; ia = ischiadic angle, in degrees; b = bipedal; q = quadrupedal; f = facultative locomotion. G1: Basal Archosauriformes; PROT = Proterosuchidae, ERYT = Erythrosuchidae. G2: Crurotarsi; PARA = Parasuchidae, AET = Aetosauria; CRO = Crocodylomorpha. G3: Pterosauria + *Scleromochlus*. G5: Sauropodomorpha; DIPLO = Diplodocidae, TITA = Titanosauridae, CAMA = Camarasauridae, BRACH = Brachiosauridae. G6+G7: Theropoda; HERR = Herrerasauridae, NEOC = Neoceratosauria, COEL = Coelophysoidea, THER = Therizinosauridae; ALLO = Allosauridae, OVIR = Oviraptoridae, ARCT = Arctometatarsalia (sensu Holtz 1994), DRO = Dromaeosauridae, ALV = Alvarezsauridae, ENAN = Enantiornithes, ICHT = Ichthyornithiformes, HESP = Hesperonithiformes, NEOR = Neornithes. G8: Ornithischia; STEG = Stegosauria. ANKY = Ankylosauria, CERA = Ceratopsia, PACH = Pachycephalosauria; HE = Heterodontosauridae, HYPs = Hypsilophodontidae; IGUA = Iguanodontidae; HADR = Hadrosauridae. LT = Lower Triassic; M-UT = Middle–Upper Triassic; LJ = Lower Jurassic; M-UJ = Middle–Upper Jurassic; LC = Lower Cretaceous; UC = Upper Cretaceous; CE = Cenozoic. Precedence of taxa drawings: 1–5, 7, 9, 10 (Kuhn 1976); 6 (Chatterjee 1978); 8, 59, 60 (Carroll 1988); 11 (Bonaparte 1981); 12 (Benton and Clark 1988); 13 (Crush 1984); 14, 16 (Kuhn 1973); 15 (Andrews 1913); 17, 19, 20 (Wellnhofer 1991); 18, 21–23 (Kuhn 1978); 24 (Sereno and Arcucci 1993); 25 (Sereno and Arcucci 1994); 26, 35, 37, 40–49, 72–86 (Weishampel et al. 1990); 27–29, 32, 33, 39 (Norman 1985); 30, 31, 36, 38 (Kuhn 1970); 34 (Novas 1994b); 50 (Ostrom 1976); 51, 55–56 (Novas 1996); 52 (Norell et al. 1993); 53 (Novas and Puerta 1997); 54 (Wellnhofer 1985); 57 (Hou 1995); 58, based on the actual specimen; 59 (Sereno and Rao 1992), reconstruction based on a cast of the actual specimen; 61 (Chiappe 1992); 63 (Rogers 1986); 64 (Proctor and Lynch 1993); 65–70 (Raikow 1985); 71 (Sereno 1991b).

No.	Age	Specimen	Orienta- tion type	Ilium ilp	Pubis pa	Ischium ia	Bound- ary pattern	Loco- motion
G1: basal Archosauriformes								
1	LT	<i>Proterosuchus</i> (PROT)	1	17	32	169	—	—
2	LT	<i>Shansisuchus</i> (PROT)	1	22	46	146	1	—
3	LT	<i>Erythrosuchus</i> (ERYT)	2	29	90	133	1	q
4	LT	<i>Vjushkovia</i> (ERYT)	1	16	50	155	1	q
5	LT	<i>Euparkeria</i>	2	24	72	153	—	b
G2: Crurotarsi								
6	UT	<i>Parasuchus</i> (PARA)	1	22	45	130	1	q
7	UT	<i>Rutiodon</i> (PARA)	1	26	44	148	1	q
8	MT	<i>Gracilisuchus</i>	2	21	73	150	—	q?
9	UT	<i>Stagonolepis</i> (AET)	2	30	75	126	—	q
10	MT	<i>Ticinosuchus</i>	1	21	52	149	1	q
11	MT	<i>Saurosuchus</i>	5	37	83	144	—	—
12	UT	<i>Postosuchus</i>	5	35	72	135	—	q
13	UT	<i>Terrestriisuchus</i> (CRO)	4	36	63	156	1	q
14	LJ	<i>Protosuchus</i> (CRO)	4	42	54	136	1	q
15	L–UJ	<i>Steneosaurus</i> (CRO)	1	29	64	134	2	q
16	CE	<i>Alligator</i> (CRO)	4	34	59	135	8	q
G3: Scleromochlus + Pterosauria								
17	UT	<i>Scleromochlus</i>	2	31	71	140	—	b
18	UJ	<i>Pterodactylus</i>	7	71	92	124	4	b
19	LJ	<i>Campylognathoides</i>	7	68	93	128	4	b
20	L–UC	<i>Anhangura</i>	5	63	94	131	2	b
21	LJ	<i>Dimorphodon</i>	5	56	87	130	4	b
22	UJ	<i>Germanodactylus</i>	7	72	79	127	—	b
23	UJ	<i>Gallodactylus</i>	7	71	84	122	—	b
G4: Dinosauriformes (including G5, 6, 7, 8)								
24	MT	<i>Lagerpeton</i>	1	29	48	148	1	b
25	MT	<i>Marasuchus</i>	1	28	57	128	1	b
G5: Sauropodomorpha								
26	UT	<i>Riojasaurus</i>	1	29	62	139	1	q
27	LJ	<i>Barapasaurus</i>	5	54	73	143	—	q
28	UJ	<i>Diplodocus</i> (DIPLO)	5	63	97	148	1	q
29	UJ	<i>Apatosaurus</i> (DIPLO)	5	58	86	144	1	q
30	L–UC	<i>Titanosaurus</i> (TITA)	5	58	79	146	1	q
31	UJ	<i>Atlantosaurus</i> (TITA)	5	53	89	144	—	q
32	UJ	<i>Camarasaurus</i> (CAMA)	5	61	89	154	1	q
33	UJ	<i>Brachiosaurus</i> (BRACH)	5	64	94	139	1	q
G6: Theropoda (including G7: Aves)								
34	UT	<i>Eoraptor</i>	5	43	79	150	—	b
35	UT	<i>Herrerasaurus</i> (HERR)	2	27	88	131	1	b
36	UJ	<i>Elaphrosaurus</i> (NEOC)	4	52	51	121	1	b
37	UJ	<i>Ceratosaurus</i> (NEOC)	5	50	77	147	—	b

TABLE 2. Continued.

No.	Age	Specimen	Orienta- tion type	Ilium ilp	Pubis pa	Ischium ia	Bound- ary pattern	Loco- motion
G6: Theropoda (including G7: Aves)								
38	UT	<i>Coelophysis</i> (COEL)	4	44	58	130	1	b
39	LJ	<i>Dilophosaurus</i> (COEL)	5	41	71	142	—	b
40	MJ	<i>Piatnitzkysaurus</i>	5	53	81	131	1	b
41	UC	<i>Segnosaurus</i> (THER)	6	60	125	141	1	b
42	UJ, LC	<i>Allosaurus</i> (ALLO)	5	51	90	137	—	b
43	UJ	<i>Compsognathus</i> (ALLO)	5	45	69	139	1	b
44	UJ	<i>Omitholestes</i>	5	55	83	136	1	b
45	UC	<i>Ingenia</i> (OVIR)	4	48	64	127	1?	b
46	UC	<i>Tyrannosaurus</i> (ARCT)	5	49	75	151	1	b
47	UC	<i>Avimimus</i> (ARCT)	5	33	76	122	1?	b
48	UC	<i>Dromiceiomimus</i> (ARCT)	5	46	82	148	1	b
49	UC	<i>Gallimimus</i> (ARCT)	4	45	60	131	1	b
50	LC	<i>Deinonychus</i> (DRO)	5	59	90	142	1	b
51	UC	<i>Adasaurus</i> (DRO)	6	55	119	132	1	b
52	UC	<i>Velociraptor</i> (DRO)	6	59	136	143	1	b
53	UC	<i>Unenlagia</i>	5	62	85	127	—	b
54	UJ	<i>Archaeopteryx</i>	7	68	106	137	3	b
55	UC	<i>Patagonykus</i> (ALV)	5	50	105	118	—	b
56	UC	<i>Shuvuuia</i> (ALV)	6	38	123	120	—	b
57	LC	<i>Confuciusornis</i>	6	58	132	151	—	b
58	LC	<i>Iberomesornis</i>	5?				—	b
59	LC	<i>Sinornis</i> (ENAN)	5	57	114	133	—	b
60	UC	<i>Ichthyornis</i> (ICHT)	6	49	153	158	4?	b
61	UC	<i>Patagopteryx</i>	6	56	134	151	4	b
62	UC	<i>Hesperornis</i> (HESP)	3	30	165	170	4?	b
63	CE	<i>Gallus</i> (NEOR)	6	49	166	167	4	b
64	CE	<i>Columba</i> (NEOR)	6	49	171	167	4	b
65	CE	<i>Struthio</i> (NEOR)	3	28	164	174	2	b
66	CE	<i>Dromaius</i> (NEOR)	6	39	172	178	4	b
67	CE	<i>Apteryx</i> (NEOR)	6	62	149	157	4	b
68	CE	<i>Pterocnemia</i> (NEOR)	6	43	172	180	4	b
69	CE	<i>Anomalopteryx</i> (NEOR)	6	52	155	170	4	b
70	CE	<i>Aepyornis</i> (NEOR)	6	39	160	169	4	b
G8: Ornithischia								
71	LJ	<i>Lesothosaurus</i>	6	52	145	148	1?	b
72	LJ	<i>Scelidosaurus</i>	6	61	134	131	1?	b
73	UJ	<i>Stegosaurus</i> (STEG)	8	68	144	142	1	q
74	UJ	<i>Kentrosaurus</i> (STEG)	6	58	129	119	1	q
75	UC	<i>Euoplocephalus</i> (ANKY)	8?	72	115	113	4?	q
76	LC	<i>Psittacosaurus</i> (CERA)	6	50	150	139	2	b
77	UC	<i>Protoceratops</i> (CERA)	6	43	166	145	2	f
78	UC	<i>Chasmosaurus</i> (CERA)	6	47	163	150	—	a
79	UC	<i>Homalocephale</i> (PACH)	6	44	157	123	4	b
80	LJ	<i>Heterodontosaurus</i> (HE)	6	58	146	145	1?	b
81	LC	<i>Hypsilophodon</i> (HYPS)	6	47	137	131	1?	b
82	UJ	<i>Camptosaurus</i>	6	51	130	133	1	f
83	LC	<i>Iguanodon</i> (IGUA)	6	49	147	136	2	f
84	LC	<i>Ouranosaurus</i> (IGUA)	6	56	134	131	2	f
85	UC	<i>Corythosaurus</i> (HADR)	6	51	162	162	2	f
86	UC	<i>Kritosaurus</i> (HADR)	6	48	157	174	2	f

the most cranial and caudal landmarks of the iliac blade (see Marcus et al. 1996 for a detailed account of shape analysis techniques).

Orientations: The Dispospace.—Two kinds of morphospaces are used in this section, theoretical and empirical (sensu McGhee 1999).

The theoretical morphospace (Fig. 2), is built by combining characters with a theoretical range of variation, allowing a raw glimpse into areas outside the data being sampled. The empirical morphospace (see Results) shows only the range of variation that is present in

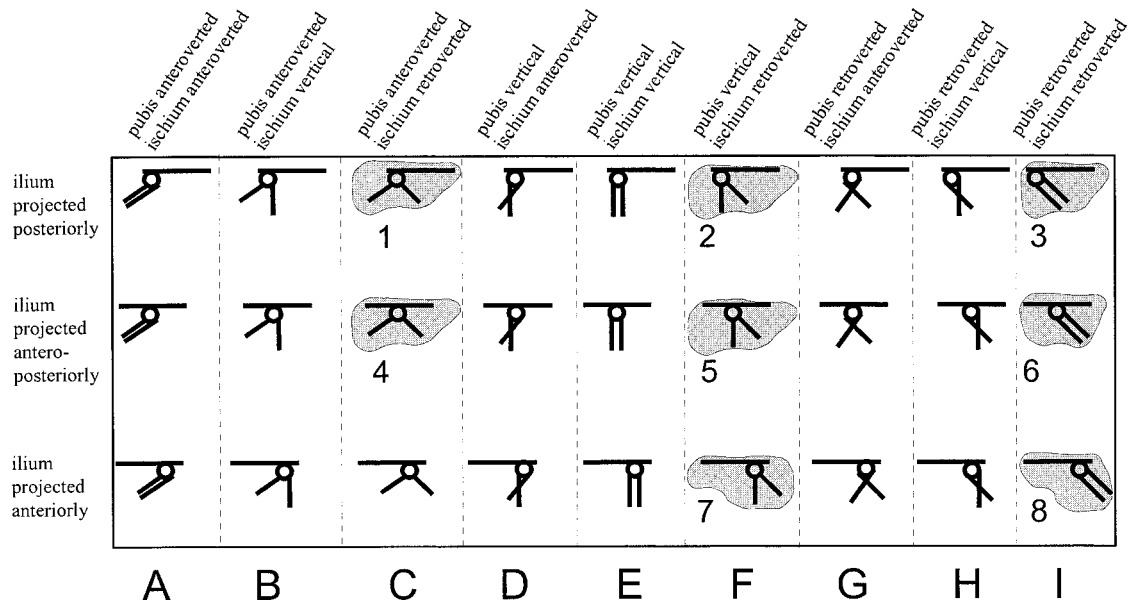


FIGURE 2. Hips abstracted by rod models to highlight the orientation of each bone and the position of the acetabulum. The dispospace of the pelvic girdle of Archosauriformes consists of the combination of the character states for each dispositional variable. The disposition of the pubis and ischium is represented together on the horizontal axis for the sake of simplification. Shaded areas show types that are present in the sample at least once. Numbers indicate those design types that occur in the sample. See text for the definition and character states of each variable.

the data; hence it can only show empty areas within the variation of the data being sampled.

The relative orientations of the ilium, pubis, and ischium are described in terms of “dispositional variables,” represented as rod models (Fig. 2). These variables can be conceived of as different modes of spatial growth. For example, one can trace the results of “growing forward” or “growing downward” for a bone that never does that in nature, as is the case of the ischium. This allows the construction of a theoretical space of arrangements, showing all the possibilities given simple rules of orientation. Furthermore, it allows the study of empirical data, angles, and distances, in a broader framework (a set of theoretical combinations, or “dispospace”).

The three dispositional variables are (1) the projection of the ilium with respect to the acetabulum, with three character states: anterior, posterior, and both; (2) the position of the pubis, with respect to the horizontal defined by the ilium, with three character states: anteroverted, vertical, and retroverted; and (3) the position of the ischium, with the same character states as for the pubis. The selection

of the character states of the variables is based on two spatial invariances present in all archosaur groups: the iliac blade always defines the main anteroposterior axis, and the pubis and ischium always orient anteroventrally and posteroventrally, respectively. There are only $3 \times 3 \times 3 = 27$ possible combinations or orientation types that do not violate this pattern.

Two angles (pubic and ischiadic) and two linear distances (iliac anteroposterior projections) were computed from seven geometrically homologous landmarks in order to assign each individual to a particular type. Landmarks were digitized using drawings for each individual taken from the literature. The line passing through landmarks 1 and 2 (iliac main direction) was used as the reference line to compute these variables. Pubic (pa): angle between the iliac line and the line passing through landmarks 4 and 5; ischiadic (ia): angle between the iliac line and the line passing through landmarks 6 and 7. Iliac projections are the distances from the perpendicular projection of landmark 3 on the iliac line and landmarks 1 and 2 for the anterior and posterior projections respectively. Distances d1

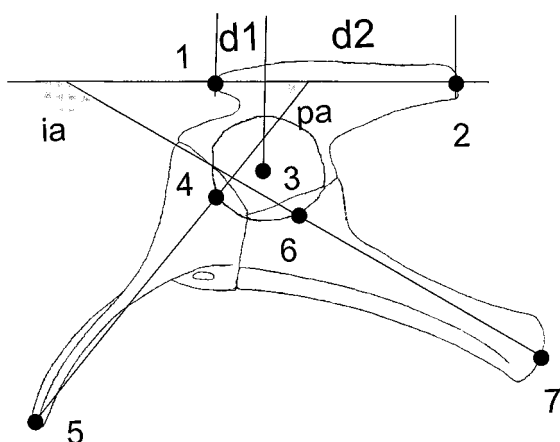


FIGURE 3. Definition of landmarks to evaluate the dispospace: 1 = most cranial part of the ilium, 2 = most caudal part of the ilium, 3 = center of the acetabulum, 4 = center of the acetabular region of the pubis, 5 = most distal edge of the pubis (disregarding pubic boot), 6 = center of the acetabular region of the ischium, 7 = most distal edge of the ischium. Abbreviation: pa = pubis angle, ia = ischiadic angle. Iliac projection (ilp) is the percentage of $d1/(d1+d2)$.

and d2 were reduced to the single value $ilp = (d1/d1+d2)100$, giving the percentage value for the anterior projection (Fig. 3). The variables pa and ilp are the axes of the empirical morphospace. A computer program was designed to compute all these angles and distances from the coordinates of the seven landmarks using elementary geometric formulas (see, for example, Bookstein et al. 1985 for a set of equations to convert landmark coordinates into angles and distances).

The archosaurian taxa used in this section (Table 2) are grouped in clades following Sereno 1991a. Orientation types were assigned to 86 taxa from all the major groups: G1: basal Archosauriformes (*Proterosuchus* + *Erythrosuchidae* + *Euparkeria* + *Proterochampsidae*); G2: Crurotarsi (*Parasuchia* + (*Ornithosuchus* + *Riojasuchus*) + *Suchia*); G3: Pterosauriforms (*Scleromochlus* + *Pterosauria*); G4: Dinosauriforms (*Lagerpeton* + *Marasuchus* + *Dinosauria*). The clade Dinosauriforms is based on Sereno and Arcucci 1993. Additionally, Dinosauria has been arranged into four major clades following Novas 1994a: G5: Sauropodomorpha; G6: Theropoda (*Eoraptor* + *Herrerasauridae* + (*Ceratosauria* + *Tetanurae*)); G7: Eumaniraptora, which includes *Dei-*

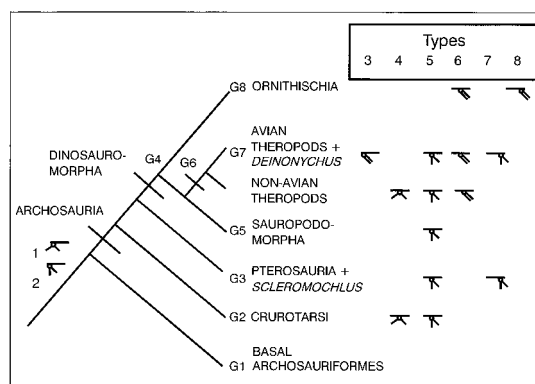


FIGURE 4. Dendrogram showing the different groups employed to evaluate the differential occupation of the morphospace and distribution of design types. This dendrogram is based on four phylogenetic hypotheses that are taxonomically congruent: (A) Groups G1, G2, G3, and G4 (tree description: (*Proterosuchus* + (*Erythrosuchidae* + (*Euparkeria* + (*Proterochampsidae* + ((*Parasuchia* + ((*Ornithosuchus* + *Riojasuchus*) + *Suchia*)) + ((*Pterosauria* + *Scleromochlus*) + *Dinosauriformes*)))))), (Sereno 1991a). The group comprising the taxa *Parasuchia*, *Ornithosuchus*, *Riojasuchus*, and *Suchia* is the clade Crurotarsi. (B) Dinosauriforms, group G4 (tree description: (*Crurotarsi* + (*Pterosauria* + (*Lagerpeton* + (*Marasuchus* + *Dinosauria*))))), (Sereno and Arcucci 1993). (C) Dinosauria, groups G5, G6, G7, and G8 (tree description: (*Pterosauria* + (*Lagerpeton* + (*Marasuchus* + (*Ornithischia* + (*Sauropodomorpha* + (*Eoraptor* + *Herrerasauridae* + (*Ceratosauria* + *Tetanurae*))))))), (Novas 1994a). (D) Aves and taxa involved in the group G7. Tree description: (*Deinonychus* + (*Archaeopteryx* + (*Alvarezsaurus* + (*Mononykus*, *Shuvuuia* + *Patagonykus*)) + (*Iberomesornis* + (*Enantiornithes* + (*Patagopteryx* + (*Hesperornithiformes* + *Ichthyornis* + *Neornithes*)))))), (Chiappe 1995; Novas 1996; Sanz et al. 1996; Chiappe et al. 1998). *Confuciusornis* has been recently proposed as the sister group of *Iberomesornis* and the remainder of Onithothoraces (Sereno 1999). Note that *Dromaeosauridae* and *Aves* are members of the clade *Tetanurae*.

nonychus + *Aves*, is part of *Tetanurae*. The clade *Aves* comprises the groups proposed by Chiappe (1995); Novas (1996); Sanz et al. (1996); Chiappe et al. (1998); and Sereno (1999); G8: Ornithischia. Figure 4 contains a dendrogram showing the relationship among these phylogenetic hypotheses. The sampling procedure was done so that it shows, at least once, all the orientation types that are present in each group. In this way, the maximum amount of variety of the different types is shown for each group. All stratigraphic ranges in which the groups occurred are present.

Connections: Boundary Patterns.—Each bone of a skeletal compound has a boundary pattern defined by the connection to other bones.

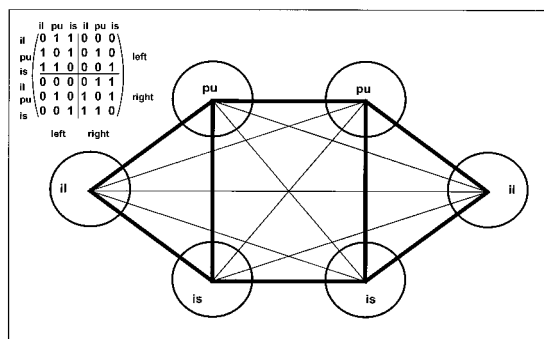


FIGURE 5. Graph that identifies in ventral view the topological relation of the elements of the pelvic girdle. There are 15 possible connections between elements, but only 8 (bold edges) occur in nature (ilium-ilium connection is a controversial point, usually done by means of sacral vertebrae). The adjacency matrix of the pelvis is a 6×6 matrix; 0 indicates nonconnected and 1 indicates connected. The matrix, then, describes the connection for each pair of bones: the upper-left submatrix describes the lateral left view; lower-right submatrix describes the lateral right view; both lower-left and upper-right submatrices describe the bilateral relationships among paired and nonpaired bones; il = ilium; pu = pubis; is = ischium.

This boundary pattern can be formalized using graph theory. Graphs are represented as a collection of vertices and edges: $G = (V, E)$, where V (the set of vertices) represents the number of elements and E (the set of edges) represents the connections between vertices. Graphs can be expressed by means of a connectivity matrix (also incidence matrix or adjacency matrix). Each element of the matrix is an account of the connection status for each pair of vertices (0, nonconnected; 1, connected). This matrix describes boundary patterns, holding relational information that specifies how the elements are connected with the remaining ones (Fig. 5). Among several estimates that this matrix may provide are the number of connections for each element, the number of parts the system is composed of, the symmetry axes, the compactedness of the pattern, and others (see, for example, Harary 1969, for an introduction to graph theory).

The number of possible edges in a graph of k elements is $k(k-1)/2$, which represents what is called a complete graph of k elements. The three-dimensional graph of the pelvis, with six elements, gives a complete graph of 15 edges. This number indicates the maximum number for possible borders without

counting double connections (e.g., an additional distal connection between pubis and ischium as occurs in many bird hips). The maximum number of connections shows those that are possible between elements. Graph theory indicates that the number of different boundary patterns (nonisomorphic graphs) that can be constructed with six elements is 156, which is the maximum number of possible patterns (a complete morphospace of connections for six elements). A subset of 16 patterns preserves bilateral symmetry and allows for disconnection between paired elements (Fig. 6). This restrictive collection of 16 boundary patterns was used as a morphospace of connections.

Results

Theoretical Proportions.—Euclidean phenetic distances in the minimum spanning tree range from 0.4 between *Compsognathus* and *Gallimimus* (most similar nearest neighbors) to 1.99 between *Herrerasaurus* and *Riojasaurus* (least similar nearest neighbors). The structure of the tree maintains the simulated morphocline as nearest neighbors (Fig. 7); whereas the hips of the actual sample stem from some of the transformed outlines. Two major groups can be distinguished, the propubic and the opisthopic. Note also that *Allosaurus* (mesopubic) is the only real hip that stems from *Deinonychus*. Because the minimum spanning tree takes into account the whole set of proportions of the outline (as coordinates), other, more subtle relations can be observed. Convergent forms group together, as is expected in a phenetic distance tree.

Theoretical Orientations.—The ischium is always oriented posteriorly, with perhaps the sole exception of the ankylosaur *Euoplocephalus*. In contrast, the pubis has a wide range of variation in spatial orientation. The ilium may extend its iliac blade anteriorly, posteriorly, or both. Ilium and pubis show all character state combinations for their dispositional variables except for one type: ilium and pubis both anteriorly projected.

The dispospace is exploited in 8 of the 27 total orientation types; that is, approximately 30% of all the possible theoretical combinations (Fig. 2). When the results for ilp (per-

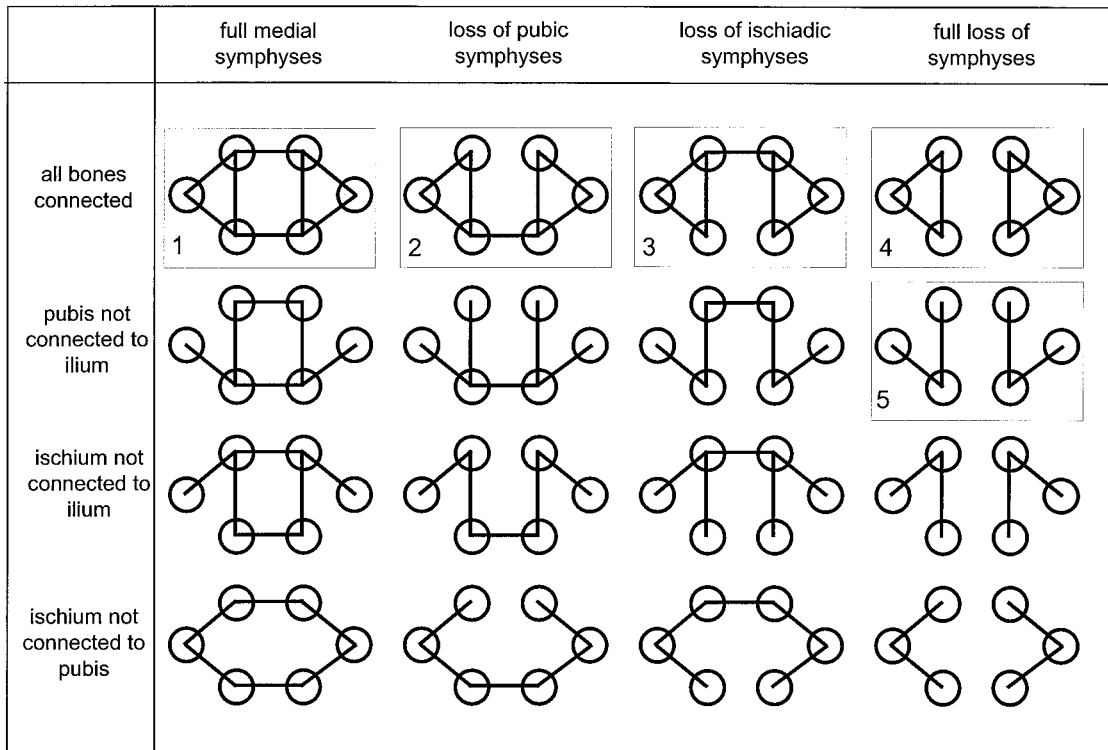


FIGURE 6. Morphospace of connections. The hips are represented in ventral view as in Figure 5. Framed and numbered graphs represent boundary patterns that are present in archosaurs.

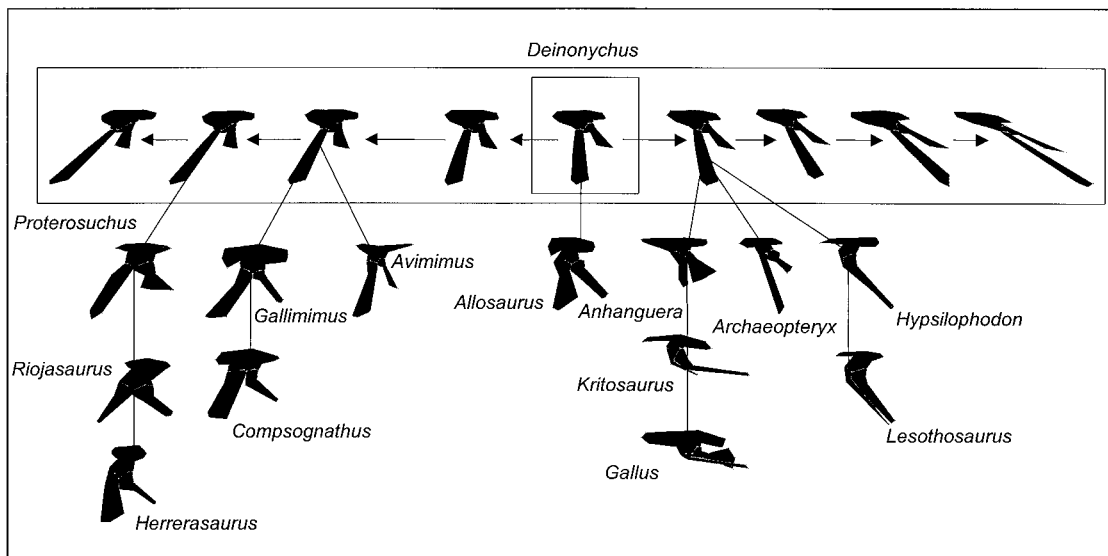


FIGURE 7. A minimum spanning tree based on the phenetic distances of the sampled hips and the affine-transformed outlines of *Deinonychus*. The arrows indicate both proximity in the sense of the minimum spanning tree and the direction of the transformation as explained in the text.

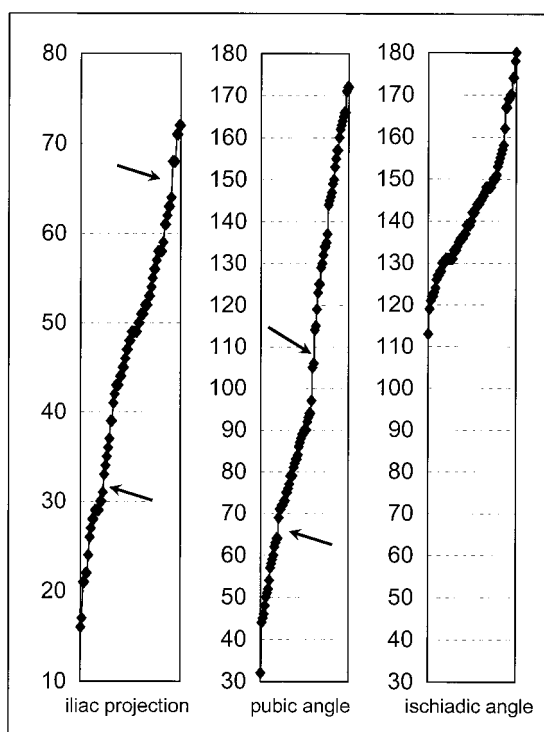


FIGURE 8. Values of iliac projection and of pubic and ischiadic angles (in degrees). The sample (Table 2) has been arranged in increasing order for each variable. Arrows point to breaks in the sample that were used to define ranges to quantify the dispositional variables.

centage of iliac expansion) and pa (pubic angle) are plotted in increasing order, several breaks can be identified in each curve (Table 2, Fig. 8). These breaks were used to define the ranges for the identification of the character states. Thus, for the iliac projections, ilp less than 33% was considered posteriorly projected; ilp between 33% and 66%, anteroposteriorly projected; and for ilp more than 66%, anteriorly projected. For the pubic angle: pro-pubic if pa less than 68 degrees, mesopubic if pa from 68 to 115 degrees, and opisthopubic if pa greater than 115 degrees. For ia, all the values were considered as retroverted ischia.

There is a range of 30 to 170 degrees for the orientation of the pubis throughout the sample, and 110 to 180 degrees for the ischiadic angle. The iliac projection has a range of 15% (posteriorly projected) to more than 70% (anteriorly projected), although most of the sample is clustered around the 50% value (anteroposteriorly projected) as shown in Figure 9.

Note that the ankylosaur *Euoplocephalus* has an ischiadic angle of 113 degrees, which could be considered as pointing downwards, rather than backwards. Also, *Archaeopteryx* (106 degrees), *Patagonykus* (106 degrees), *Sinornis* (114 degrees), *Adasaurus* (119 degrees), and *Shuvuuia* (123 degrees) are situated in the border between a vertical and backwardly oriented pubis. A striking result is that 75% of the ornithischian sample shows the pubic angle greater than the ischiadic angle; that is, there is a tendency toward a crossing of both elements when they are both retroverted.

There is a weak positive correlation between ilp and pa ($r = 0.7$). However, this trend (the greater the anterior projection of the ilium the more retroverted the pubis) occurs only while the pubis is either anteroverted or vertical. In contrast, the relation between the pubic angle and the projection of the ilium shows the opposite tendency (a poor negative correlation; $r = -0.59$), in both retroverted groups (ornithischians and birds).

Phylogenetically, the distribution of types 1 and 2 appears in the basal taxa and in the basal nodes of all considered groups (Fig. 10). Type 5 appears convergently in all the archosaurian groups except in ornithischians and birds. Type 6 is an exclusive convergence of ornithischians and birds, but also some non-avian theropods show this type. Type 8 seems to appear only in some thyreophoran ornithischians. Crurotarsi (G2) has added types 4 and 5 to their primitive arrangement, types 1 and 2; and Pterosauria has added types 5 and 7 (Table 2, Fig. 5). Dinosauromorpha (G4) exploits all types: theropods (G6-G7), including birds, exploit six, whereas the non-avian theropods exploit four; sauropodomorphs (G5) exploit two types and ornithischians (G8) exploit two others.

Regarding geologic time, the exploitation of types increases from two types in the Lower Triassic to six types by the Middle-Upper Jurassic. The Cenozoic shows a decrease to three types. Thus, only the opisthopubic types of modern birds (types 3 and 6) and the triradial type of modern crocodiles (type 4) are found after the K/T boundary. Type 1 extends from the Lower Triassic to the Middle-Upper Jurassic, while type 2 disappears in the Mid-

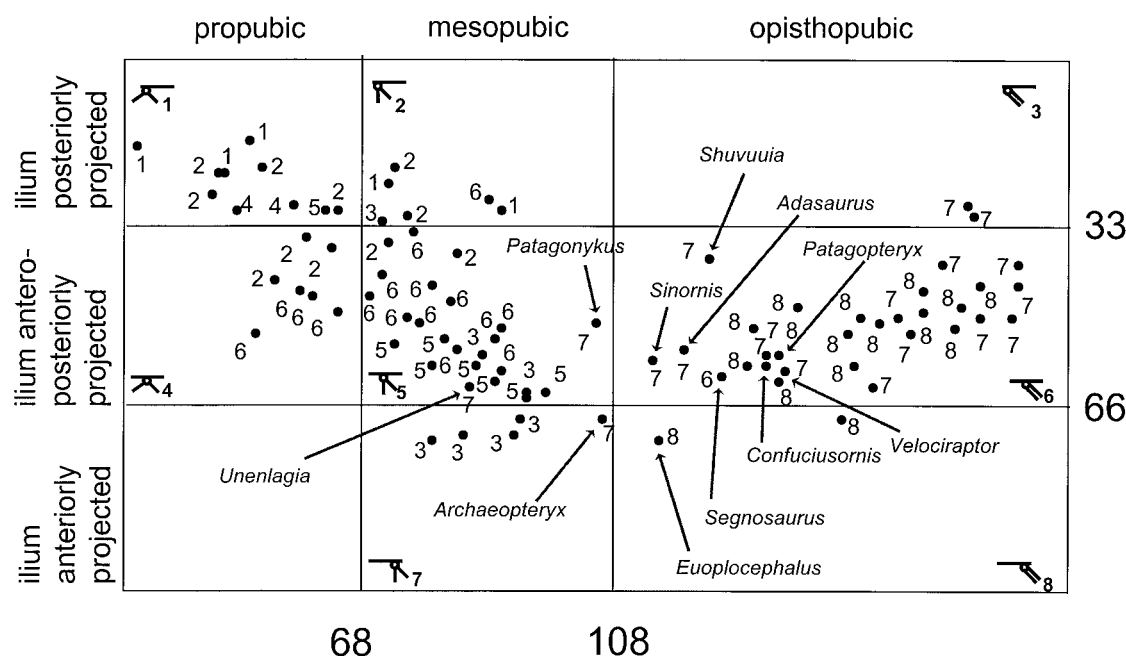


FIGURE 9. Empirical morphospace. Scatter plot of ilp (y-axis, iliac projection, in percentages) versus pa (x-axis, pubic angle, in degrees). Numbers indicate clade for each individual of the sample (Fig. 7). Note a change of slope at approximately 115 degrees.

dle–Upper Triassic. By the Lower Cretaceous both primitive types have disappeared (Fig. 10).

Orientation types and locomotor patterns are not correlated. There is a clear overlapping among types present in quadrupeds and bipeds. Thus, type 5 occurs in quadrupedal suchians and sauropods as well as bipedal pterosaurs and theropods, and type 6 in facultatively bipedal hadrosaurs, quadrupedal stegosaurs, and flying and cursorial birds. This convergence of orientation types highlights that locomotor types are not tied to specific pelvic arrangements. The case for dinosaurs is even more clear. They all maintain an erect posture and yet both bipedalism and quadrupedalism are found with the same orientation type (Table 2).

Theoretical Connections.—Of the 15 possible connections between bones, only eight occur in nature: six connections account for the ilium-ischium-pubis borders (conforming the acetabulum) in both sides and two occur between homologous left-right bones (pubic and ischiadic symphyses). The connection between paired ilia is not counted, as it involves

the fusion of sacral vertebrae such as in the avian synsacrum.

The morphospace of connections is exploited in five patterns. There are two invariances, both involving the ischium, which always connects to both the ilium and the pubis. All the remaining connections are variable, including the medial symphyses. All groups have connection type 1, with the exception of pterosaurs and avian theropods. Ornithischians lost also one or both medial symphyses, but they retained type 1. Exploitation by time indicates that fully connected pelves seem to be characteristic of Triassic Archosauriformes and retained through the Cretaceous, whereas three additional types of boundary patterns are found in the Cenozoic (types 8, 4, and 2). According to our data, a trend toward the loss of symphyses on the ventral elements occurred in the transition from non-avian to avian theropods. Thus, dromaeosaurids have all bones weakly connected by medial symphyses (type 1); *Archaeopteryx*, the basal member of Aves, has lost the connection between the ischia (type 3); and most Ornithurae (except *Struthio*) have lost both connections (type 4).

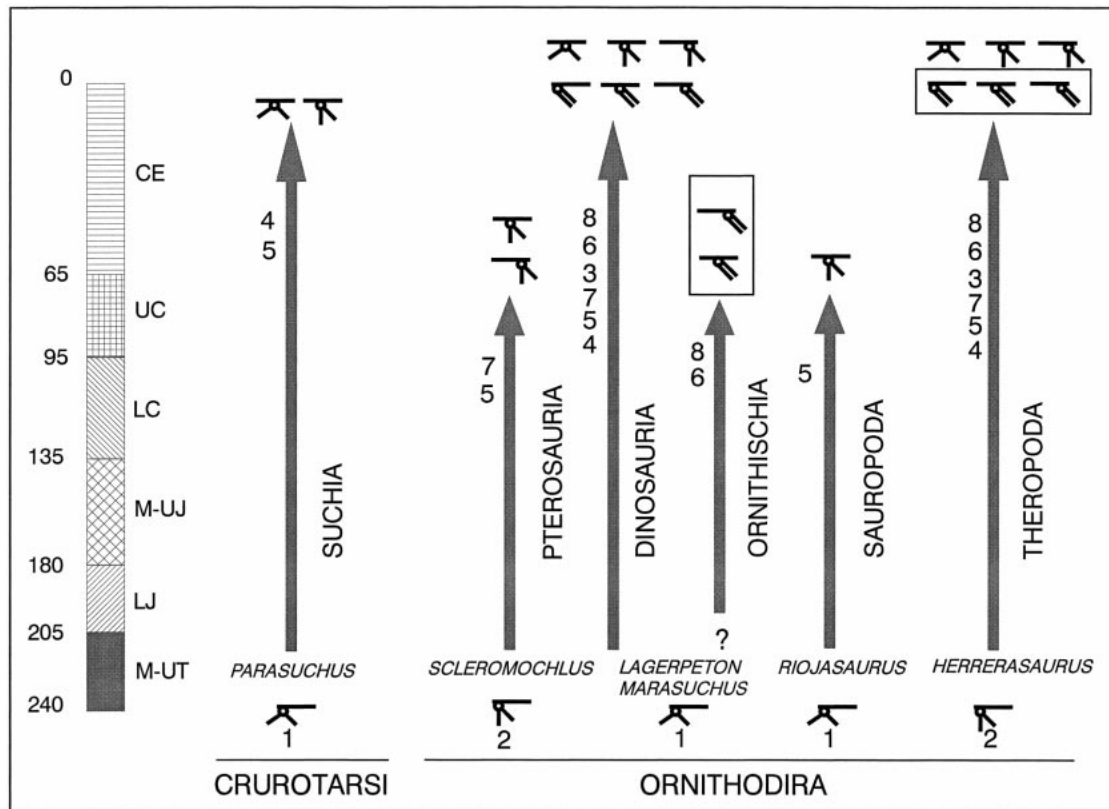


FIGURE 10. Orientation types per group and time of the pelvic girdle of Archosauriformes. Top part shows the number of types for each group. Bottom part shows rod models of each exploited type per group. Note that types 1 and 2 are distributed exclusively at the base of each group (Suchia, Pterosauria, Sauropoda, and Theropoda). All genera that show these types (1 and 2) appeared in the Middle or Upper Triassic (240 to 205 Ma; Table 2). Question mark denotes the absence of a known ornithischian basal taxon bearing type 1 or 2. Types that have lost gastralia are framed, to emphasize this convergence in ornithischians and birds.

The loss of connections for the same number of elements involves a loss in the compactedness of the graph, defined as the ratio between number of possible connections (15) and number of actual connections. These losses represent a change in the compactedness of the pelvis from 0.53 (8/15) to 0.4 (6/15).

Discussion

The three levels of abstraction explored in this paper introduce a theoretical morphology perspective to analyze the production and possible variations of the archosaur hip. Each morphospace provides a framework by which to search for levels of morphological constraints that act on the final fabrication of the pelvis and where hypotheses and predictions

that are mutually independent can be suggested and contrasted.

The final morphology of an organism is a direct product of developmental patterning and growth. The analysis of the possible morphological constraints for the final structures found in various taxa reveals the different ontogenetic paths followed by each one. The condensation patterns of mesenchyme precursors of the three hip bones (a cell-to-cell boundary interaction) do not predetermine the final orientation of the three paired bones, but only their general position in the body of the growing embryo. Furthermore, the three bones chondrify in separate centers in the developing chick embryo (Romanoff 1960; Starck 1993), thus having freedom to become orient-

ed in any direction. The puboischiadic fenestra also contributes to this freedom to rotate in anterior or posterior directions, while the symphyses act as mediolateral spatial constraints.

Proportions.—Problems of proportions have been evaluated by means of a coordinate abstraction of the pelvic outline, showing a theoretical path of change and its relation to the actual variation in real hips. This procedure has readily shown the strong convergent phenomena of the different lineages of archosaurs for the proportions of the hip (i.e., the ornithischian/bird convergence). The mesopubic hip of *Deinonychus* undergoes, under the effects of the affine model of change, both the anteroversion and retroversion of the pubis. The morphocline used to build the minimum spanning tree is a trend in both directions accomplished by means of a simple change of proportions. The morphological homologous relationships of the components of each simulated image are an identity relationship in mathematical terms. Every change in the morphology of the transformed images is correlated with the other changes, which leads one to speculate that a phenomenon of correlation may be involved in the process behind this macroevolutionary sequence. As the ilium is projected anteriorly, the pubis is retroverted, whereas the posterior projection of the ilium correlates with the anteroversion of the pubis. This correlation can be thought of as a multivariate allometry function, in which the variables are the coordinates. Because evolutionary trajectories from one form to another can follow different nonlinear paths, the simulated transformation shows only just one of these paths, which must be tested against independent phylogenetic or functional criteria.

In a more conceptual interpretation of this exercise, the simulation of change by means of a mathematical transformation raises the following points regarding its descriptive power and the sort of biological predictions that can be made. The morphocline is a description of a trend if a correspondence with an ontogenetic sequence and/or an independent phylogenetic series can be established. If this holds true, then the morphocline might (1) simulate intermediate forms; (2) predict ear-

ly/late ontogenetic stages or descendant/ancestral forms; (3) propound automatically the criteria for a transformation series (ordination of each state of the character); or (4) establish a mathematical relationship between those forms that belong to the morphocline, which ultimately boils down to a hypothesis of restrictive change. This offers a model to be tested against the neutral model of random change using additional biological evidence.

Orientations.—Pubic orientations are not associated with specific locomotor patterns (Table 2). Both running birds and flying birds show opisthopubic orientation. Ornithischians, which had a bipedal ancestor, have modified their locomotion in some lineages, acquiring a quadrupedal stance (e.g., Thyrophora), but the pelvis remained opisthopubic. Hence, the orientation of the bones of the pelvic girdle cannot be justified as adaptations to locomotor habits. Even among those orientations of the dispospace that are not realized in nature, we cannot find a well-supported justification for disregarding them on the grounds of possible functional inadequacy. For example, among those types that show crossing between pubis and ischium (see Fig. 2, columns D, G, and H), it is unclear that an alleged need for a specific pattern of muscular attachments will make these nine crossing types functionally inviable. Moreover, changes in muscular attachment areas are not uncommon, e.g., the *M. ambiens* in birds (Rai-kow 1985; see McKittrick 1993 for other examples), or the *M. puboischiofemoralis internus* in ankylosaurs (Coombs 1979). Also, as shown by the results of the empirical morphospace, a slight crossing between the pubis and ischium occurs in ornithischians and birds when both elements are retroverted (type 6). In fact, the case of *Euoplocephalus* suggests that a type with crossing retroverted pubis and vertical ischium might be functionally viable. The common feature of the nonoccurrent types of the dispospace, including columns A, B, D, E, G, and H, is the nonretroversion of the ischium, which might be sufficient to explain their nonoccurrence. This invariant reflects the intimate ontogenetic relationship of the ischium to the cloacal system.

The orientation types 1 and 2 are primitive

both in temporal scale and in phylogenetic terms of each principal clade. In contrast with other major tetrapod lineages such as mammals (Lessertisseur 1966), the origin of the different hip architectures early throughout the archosaur phylogeny cannot be viewed as a morphocline, but as a radiation. Both types (1 and 2) should be considered as primitive orientations in Archosauria, occurring almost exclusively in the fossil record during the Triassic, while the remaining ones appear during the Lower Jurassic. From these ancestral conditions types 4, 5, and 7 have been reached through a modification of the iliac projection and the pubic orientation. These types show convergence (i.e., they appear independently in Suchia, Pterosauria, Sauropoda, and non-avian Theropoda). Furthermore, within a more inclusive lineage there is no preferential type (e.g., within Arctometatarsalia, types 4 and 5 are present). In contrast, once a retroverted pubis has appeared (types 3, 6, and 8), no reversions occur to other orientation types within the lineages that have acquired these hips.

The relationship among orientation types 4, 5, and 7 is a compromise between the iliac projection and the opisthopubic and mesopubic disposition. The theoretical morphocline simulated from the pelvic girdle of *Deinonychus* shows the existence of a correlation that associates changes between the proportion of the ilium and the orientation of the pubis. This relation has been shown by different authors, mostly to suggest that there is a correlation between an anterior projection of the ilium and the retroversion of the pubis (Romer 1923; Charig 1972; Walker 1977). The analyses we carried out between the *ilp* and *pa* values reveal that the scenario is not that simple. Thus, there seems to be a general positive correlation between a more anteriorly projected ilium and the pubic angle only while the pubis is either anteroverted or vertical (Fig. 9). In contrast, this relation shows the opposite tendency in ornithischians and birds. One must conclude that once a retroverted condition is reached the dispositional relation between the pubis and the anterior expansion of the ilium disappears. The nonoccurrence in nature of the last type of column C (Fig. 2) also suggests

an equivalent explanation, since here the covariation between pubis and ilium has been altered (the ilium is projected anteriorly and the pubis is anteroverted).

Connections.—The graph models of the pelvis are conservative. Bilateral symmetry is always preserved and the ischium never loses contact with both ilium and pubis (Fig. 6). In contrast, the pubis may lose contact with the ilium as in modern crocodiles (type 8), in which the pubis connects to the ilium via a cartilage, the *pars acetabularis*. The connection type with a full set of medial symphyses is the primitive type (type 1). Phylogenetically, this type is also present in the basal members of each lineage. The reduction of compactedness from the primitive type does not reflect a loss of structural strength of the pelvis. On the contrary, in pterosaurs, ornithischians, and birds the reduction of compactedness is accompanied by an increase in the number of sacral vertebrae, which overall supposes a “dorsalization” of the whole pelvic area. In contrast, extant crocodiles have lost both bony symphyses, without increasing the number of sacral vertebrae. This group forms cartilaginous medial connections, forming a ventrally closed pelvic girdle like the primitive type.

The transition from non-avian theropods to birds shows a clear tendency to a total loss of the symphyses. This trend supports what we have already discussed in the morphocline exercise. It also has some significance regarding the retroversion of the pubis in birds because the loss of symphyses frees the paired elements to be pushed backwards. The maintenance of the ilioischadic connection as an invariance in all boundary patterns reflects the same constraint as seen in the orientations. The propubic orientation types are connection types 1, 2, and 8; mesopubic orientation types occur in connection types 1, 2, 3, and 4; and opisthopubic orientation types occur in types 1, 2, and 4. All dispositional types (except 3 and 7) occur within the primitive fully connected type.

The loss or addition of a vertex introduces a novelty (autapomorphy) in some archosaurian groups (see Müller 1990). The loss of a vertex (which involves the loss of two connec-

tions) occurs in the Ankylosauria. Only the pubis has disappeared in some taxa, but never the ischium or ilium. On the other hand, extra pubic elements have appeared in different groups (epipubis in ornithischians and pterosaurs or pars acetabularis in modern crocodiles), adding one vertex and two connections to their graph models. The addition of a new vertex in crocodilians allowed the emergence of a mobile mechanism in the pelvic girdle of the archosaurs from the static compound discussed so far. The mobility of the pubis is determinant and unique for the pistonlike ventilation of crocodilians. In this sense, the pelvic girdle of modern crocodiles became totally differentiated from all the propubic archosaurian pelvises. This is in contrast to the idea of Ruben et al. (1997), who postulated similar ventilatory functions between crocodiles and theropods on the basis of orientation of the pubis, neglecting the fact that the pubis is mobile only in crocodiles (Farmer and Carrier 2000), while in theropods it is firmly connected to both ilium and ischium.

The Problem of the Convergence of the Pubis.—The different architectural patterns of archosaur hips have traditionally been considered as having originated in response to adaptive locomotor factors, owing to the reaccommodation of muscles that insert in pelvis, tail, and hindlimb (see Galton 1969; Charig 1972; and Walker 1977). However, the convergence of the pubis in ornithischians and birds is a morphological pattern that has escaped a suitable explanation. Perhaps what is needed is to add an external structure (a hidden variable) that could be related to the retroversion process during the embryonic development of the pelvis. Both the absence of gastralia and the lack of anterior projection of the pubic foot could be directly related to pubic convergence. A link between developmental sequences and the observed phylogenetic patterns could be made, adding a plausible “developmental hypothesis.” Thus, it has been shown that during the developmental stages of bird embryos (Goodrich 1986, and references therein; Starck 1993) the pubis rotates from a vertical to the retroverted condition shown in adults. However, in crocodiles, although the early pubis

also orients vertically, it acquires a characteristic anteroverted position (Goodrich 1986).

It could be hypothesized, in the light of our results, that a pulling force is needed to counteract pushing forces (e.g., those exerted by the posterior abdominal mass and cavities) that would provoke the rotation of the pubis during development (Fig. 11, bottom). This pulling force could be due to the gastral basket and its associated hypaxial muscles. Then, a correlation between presence of gastralia and pro- and mesopubic orientations should be expected. The taxa revised in our sample show that the propubic archosaurian pelvic girdles have associated gastralia, while the opisthopubic archosaurians (Ornithischia and Ornithurae) do not (Fig. 11, top). Some groups, e.g., sauropods and dromaeosaurs, show some conflicts with the involvement of gastralia in maintaining the pubis in anteroverted or vertical positions. In pro- and mesopubic forms such as sauropods, the existence of gastralia is currently being revised (see Filla and Redman 1994; J. S. McIntosh personal communication 1996). If the presence of gastralia in sauropods is confirmed, the involvement of these bones in keeping the pubis in a meso-propubic orientation will have better support. An opisthopubic condition is reached in Therizinosauroida (“segnosaurs”), in dromaeosaurid theropods such as *Adasaurus* and *Velociraptor*, and in the Alvarezsauridae (*Shuvuuia*), as well. The existence of Therizinosauroida and dromaeosaurs with avian pelvic design (type 6) is not phylogenetically incongruent (see Xu et al. 1999 and Sereno 1999 for the phylogenetic position of “segnosaurs”). Regarding *Archaeopteryx*, there has been controversy about the nature of its pelvis, especially its actual pubic angle. It has been considered, mainly on the basis of the Berlin and Maxberg specimens, that its pubis is retroverted as in modern birds (for a recent paper taking this point of view, see Ruben et al. 1997). However, Wellnhofer (1985) has argued against this idea, pointing out that the pelvis of this ancient bird is more reptilelike than birdlike. Our data support Wellnhofer’s view, giving a mesopubic condition for this primitive bird (pa = 106). The *Velociraptor* specimen described in Norell and Makovicky

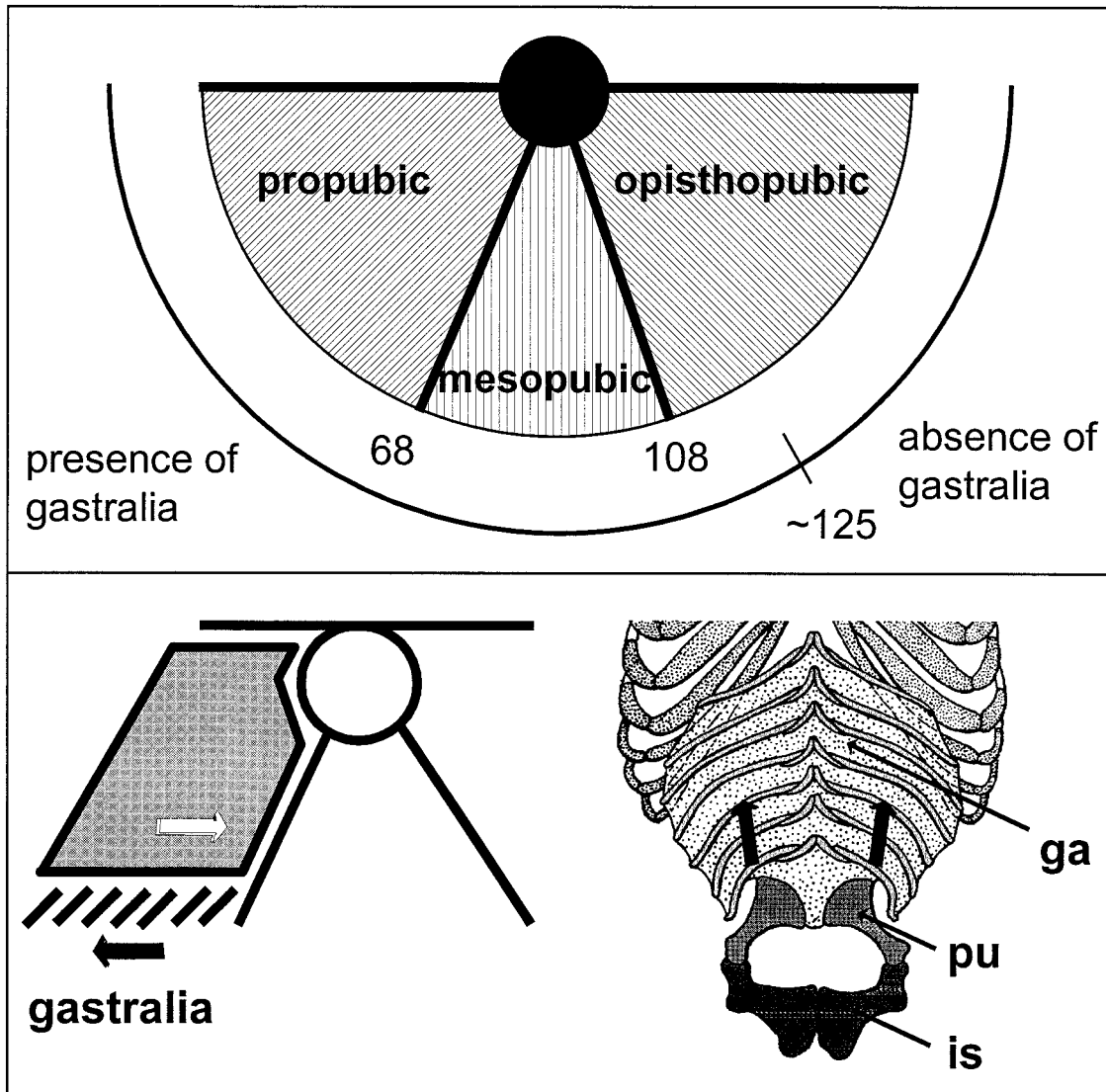


FIGURE 11. Above, range of variation of the pubic angle and presence of gastralia in archosaurs. Up to approximately 125 degrees, all taxa have gastralia. Below, left, hypothetical pushing and pulling forces involved in the orientation of the pubis during development; right, ventral view of the gastral apparatus from an extant adult crocodile; arrows indicate the direction of the pulling force (after Romer 1956).

(1997) has been reported as having a pubic angle of 155 degrees; however, using our landmarks, the angle falls down to 130 degrees, which is closer to other dromaeosaurs. Finally, lack of anterior projection of the pubic foot is common to some taxa that exhibit mesopubic hips, such as *Unenlagia*, *Archaeopteryx*, and *Sinornis*, and to those taxa that show a slight retroversion, such as the ones mentioned above. All these taxa might have had the gastral basket less strongly attached to the pubic foot

(owing to the absence of the anterior projection).

Conclusions

Formalisms are needed in macroevolutionary studies; they provide objective frameworks that are independent from the nature of the elements and relationships they represent. We have shown theoretical views applied to the pelvic girdle in archosaurs, as an example for a much broader application in the mor-

phological organization of the tetrapod skeleton. Three levels of abstraction have been analyzed to assess evolutionary aspects of the archosaur pelvic girdle: proportion, orientation, and connection. Each one has shown a different level of information that throws new light on the patterns of change, as well as on the disparity reached by this tetrapod skeletal structure. A hidden variable, the gastralium, has been hinted at as part of a plausible developmental hypothesis to account for the retroversion of the pubis in both ornithischians and birds.

Simulations are powerful tools to help understand the possibilities of morphological change from a strictly geometric view. When other biological aspects are introduced in the geometric model of transformation, new insights can be obtained regarding the biological processes underlying the change. The morphocline generated with mathematical manipulations of the outline of the hip of *Deinonychus* has shown a constraint based on the positive correlation between the anterior expansion of the ilium and the retroversion of the pubis, whereas the empirical data of the dispace show that this correlation reverts in ornithischians and birds. The possibilities for applying mathematical transformations to known outlines in order to simulate morphoclines are enormous, and the gain in theoretical insights about form change is worth the effort.

The character states of the dispace provide a particularly simple and operational framework to assess disparity and patterns of variation of the orientation types for the pelvic girdle. Once the novelty of a triradiate pelvic girdle appears in archosaurs, the relation between the growth of both ilium and pubis delimits the patterns of variation of pubic orientation. Pro- and mesopubic orientations are common homoplasies in the archosaurian evolution, whereas, once the opisthopubic orientation emerges, reversals never occur. The comparison between the variation of the natural types and those patterns that have not been realized in nature easily reveals morphological limitations of the pelvic girdle (such as the invariant retroverted ischium). This interplay between the empirical evidence and the models prompts the initiation of a thorough

exploration of the phenotypic organization and the elaboration of morphogenetic models in order to try to explain the observed patterns.

The analysis of boundary patterns has several desirable properties that should be included in modeling morphology: (1) It is grounded on the "principle of connections," a powerful tool for the assessment of homological relationships. (2) It integrates the information of the whole skeletal part, because its most important feature is to be relational. This point is critical, because morphological characters are often analyzed without consideration of their interrelationships, but rather as independent features. (3) It is efficiently represented by graphs, which are well understood in mathematical terms, as well as intuitive in their graphical display. (4) The connections among edges could also be viewed as input-output relationships, perhaps developmental mechanisms (for which the usage of directed graphs will be necessary). (5) Ontogenetic and evolutionary change of connections can be evaluated as matrix operations, offering an economic way to formalize these processes.

Finally, we have arrived at a developmental hypothesis after looking at the properties of the pelvic system as seen from three theoretical perspectives. Our hypothesis delimits a skeletal region (a "hidden variable") and suggests a possible causal developmental mechanism for pubic orientation in archosaurs. However, the process is not totally understood. The gastralium are embedded in the ventral musculature and attached to the distal part of the pubis in unknown ways in some extinct archosaurs. A complex set of mechanisms may be involved during the early development of the archosaur embryo, involving pushing and pulling forces at different times and places. So far, proposed models to explain convergences in specific structures have been mostly based on mechanisms that are able to produce heterochronies. But these explanations can be made only when the ontogenetic trajectory of the various taxa of a lineage are known. Further experimental research on the embryonic development of the only surviving archosaurs, birds and crocodiles, will provide

the necessary clues to either support or reject our developmental hypothesis.

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Literature Cited

- Alberch, P., and E. A. Gale. 1985. A developmental analysis of an evolutionary trend: digital reduction in amphibians. *Evolution* 39:8–23.
- Alexander, R. Mc. N. 1989. Dynamics of dinosaurs and other extinct giants. Columbia University Press, New York.
- Andrews, C. W. 1913. A descriptive catalogue of marine reptiles of the Oxford clay: Crocodiles, Part II. Monography. British Museum of Natural History, London.
- Benton, M. J., and J. M. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodylia. Pp. 295–338 in M. J. Benton, ed. The phylogeny and classification of the tetrapods, Vol. 1. Amphibians, reptiles, birds. Clarendon, Oxford.
- Bonaparte, J. F. 1981. Descripción de "*Fasolasuchus tenax*" y su significado en la sistemática y evolución de los Thecodontia. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia* III(2):55–101.
- Bookstein, F., B. Chernoff, R. Elder, J. Humphries, G. Smith, and R. Strauss. 1985. Morphometrics in evolutionary biology. Academy of Natural Sciences of Philadelphia Special Publication 15.
- Carroll, R. L. 1988. Vertebrate paleontology and evolution. W. H. Freeman, New York.
- Chapman, R. E., and D. Rasskin-Gutman. 2001. Quantifying morphology. In D. E. G. Briggs and P. R. Crowther, eds. *Paleobiology II*. Blackwell Science, Malden, Mass. (in press).
- Charig, A. J. 1972. The evolution of the archosaur pelvis and hind-limb: an explanation in functional terms. Pp. 121–155 in K. A. Joysey and T. S. Kemp, eds. *Studies in vertebrate evolution*. Winchester, New York.
- Chatterjee, S. 1978. A primitive parasuchid (phytosaur) reptile from the Upper Triassic Maleri formation of India. *Palaeontology* 21:83–127.
- Chiappe, L. M. 1992. Osteología y sistemática de *Patagopteryx delferrariisi* Alvarenga y Bonaparte (Aves) del Cretácico de Patagonia. Filogenia e historia biogeográfica de las aves cretácicas de América del Sur. Ph.D. dissertation. Universidad Nacional de Buenos Aires, Buenos Aires.
- . 1995. The first 85 million years of avian evolution. *Nature* 378:349–355.
- Chiappe, L. M., M. A. Norell, and J. M. Clark. 1998. The skull of a relative of the stem-group bird *Mononykus*. *Nature* 392:275–278.
- Coombs, W. P., Jr. 1979. Osteology and myology of the hindlimb in the Ankylosauria (Reptilia, Ornithischia). *Journal of Paleontology* 53:666–684.
- Crush, P. J. 1984. A Late Upper Triassic sphenosuchid crocodilian from Wales. *Palaeontology* 27:131–157.
- Farmer, C. G., and D. R. Carrier. 2000. Pelvic aspiration in the American alligator (*Alligator mississippiensis*). *Journal of Experimental Biology* 203:1679–1687.
- Fillia, J., and P. D. Redman. 1994. *Apatosaurus yahnahpin*: a preliminary description of a new species of diplodocid dinosaur from the Late Jurassic Morrison Formation of Southern Wyoming, the first sauropod dinosaur found with a complete set of "belly ribs." Pp. 159–178 in Wyoming Geological Association Guidebook, 44th Annual Field Conference. Dinomation International Society, Boulder, Colo.
- Galton, P. M. 1969. The pelvic musculature of the dinosaur *Hypsilophodon* (Reptilia: Ornithischia). *Postilla* 131:1–64.
- Gatesy, S. M. 1995. Functional evolution of the hindlimb and tail from basal theropods to birds. Pp. 219–234 in J. J. Thomason, ed. *Functional morphology in vertebrate paleontology*. Cambridge University Press, Cambridge.
- . 1997. An electromyographic analysis of hindlimb function in *Alligator* during terrestrial locomotion. *Journal of Morphology* 234:197–212.
- Gatesy, S. M., and K. P. Dial. 1996. Locomotor modules and the evolution of avian flight. *Evolution* 50:331–340.
- Gauthier, J. A., A. G. Kluge, and T. Rowe. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4:105–209.
- Goodrich, E. S. 1986. Studies on the structure and development of vertebrates. University of Chicago Press, Chicago.
- Goodwin, B. C. 1963. Temporal organization in cells: a dynamic theory of cellular control processes. Academic Press, London.
- Gould, S. J. 1991. The disparity of the Burgess Shale arthropod fauna and the limits of cladistic analysis: why we must strive to quantify morphospace. *Paleobiology* 17:411–423.
- Harary, F. 1969. Graph theory. Addison Wesley, Reading, Mass.
- Hou, L. 1995. Morphological comparisons between *Confuciusornis* and *Archaeopteryx*. Pp. 193–201 in A. Sun and Y. Wang, eds. VI Symposium on Mesozoic terrestrial ecosystems and biota, Short papers. China Ocean, Beijing.
- Kuhn, O., ed. 1970. Encyclopedia of paleoherpetology, Part 14. Saurischia. Gustav Fischer, Stuttgart.
- , ed. 1973. Encyclopedia of paleoherpetology, Part 16. Crocodylia. Gustav Fischer, Stuttgart.
- , ed. 1976. Encyclopedia of paleoherpetology, Part 13. Thecodontia. Gustav Fischer, Stuttgart.
- , ed. 1978. Encyclopedia of paleoherpetology, Part 19. Pterosauria. Gustav Fischer, Stuttgart.
- Lessertisseur, J. 1966. L'angle ilio-sacré des reptiles aux mammifères: son interprétation, son intérêt paléontologique. In *Problèmes actuels de paléontologie, evolution des vertébrés. Colloques Internationaux du Centre National de la Recherche Scientifique* 163:475–481.
- Lotka, A. J. [1924] 1956. Elements of mathematical biology. Reprint, Dover, New York. (Originally published as Elements of physical biology, Williams and Wilkins, Baltimore.)
- Mandelbrot, B. B. 1983. The fractal geometry of nature. W. H. Freeman, New York.
- Marcus, L. F., M. Corti, A. Loy, D. Slice, and G. Naylor. 1996. Advances in morphometrics. NATO ASI Series, A 284. Plenum, New York.
- McGhee, G. R., Jr. 1999. Theoretical morphology: the concepts and its applications. Columbia University Press, New York.
- McKittrick, M. C. 1993. Trends in the evolution of the hindlimb musculature in aerially foraging birds. *Auk* 110:189–206.
- Müller, G. B. 1990. Developmental mechanisms at the origin of morphological novelty: a side-effect hypothesis. Pp. 99–130 in M. H. Nitecki, ed. *Evolutionary innovations*. University of Chicago Press, Chicago.

- Norell, M. A., and P. J. Makovicky. 1997. Important features of the dromaeosaur skeleton: information from a new specimen. *American Museum Novitates* 3215.
- Norell, M. A., L. M. Chiappe, and J. Clark. 1993. New limb on the avian family tree. *Natural History* 102(9):38–42.
- Norman, D. 1985. *The illustrated encyclopedia of dinosaurs*. Salamander Books, London.
- Novas, F. E. 1994a. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *Journal of Vertebrate Paleontology* 13:400–423.
- . 1994b. Origen de los dinosaurios. *Investigación y Ciencia* 217:52–59.
- . 1996. Anatomy of *Patagonykus puertai* (Theropoda, Avialae, Alvarezsauridae), from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology* 17:137–166.
- Novas, F. E., and P. F. Puerta. 1997. Alvarezsauridae, Cretaceous basal birds from Patagonia and Mongolia. *Memoirs of the Queensland Museum* 39:675–702.
- Ostrom, J. H. 1976. On a new specimen of the Lower Cretaceous theropod dinosaur *Deinonychus antirrhopus*. *Breviora* 439:1–21.
- Parrish, J. M. 1986. Locomotor adaptations in the hindlimb and pelvis of the Thecodontia. *Hunteria* 1(2):2–35.
- Proctor, N. S., and P. J. Lynch. 1993. *Manual of ornithology: avian structure and function*. Yale University Press, New Haven, Conn.
- Raikow, R. J. 1985. Locomotor system. Pp. 57–147 in A. S. King and J. McLelland, eds. *Form and function in birds*, Vol. 3. Academic Press, London.
- Rashevsky, N. 1944. Studies in the physicomathematical theory of organic form. *Bulletin of Mathematical Biophysics* 6:1–59.
- Rasskin-Gutman, D. 1995. *Modelos geométricos y topológicos en morfología. Exploración de los límites del morfoespacio afín. Aplicaciones en paleobiología*. Ph.D. dissertation. Universidad Autónoma de Madrid, Madrid.
- . 1997. Pelvis, comparative anatomy. Pp. 536–540 in P. J. Currie and K. Padian, eds. *Encyclopedia of dinosaurs*. Academic Press, San Diego.
- Rasskin-Gutman, D., and A. D. Buscalioni. 1996. Affine transformation as a model of virtual form change for generating morphospaces. Pp. 169–178 in Marcus et al. 1996.
- Rogers, E. 1986. *Looking at vertebrates: a practical guide to vertebrate adaptations*. Longman Group Limit, Essex.
- Romanoff, A. L. 1960. *The avian embryo*. Macmillan, New York.
- Romer, A. S. 1923. Crocodilian pelvic muscles and their avian and reptilian homologues. *Bulletin of the American Museum of Natural History* 48:533–552.
- . 1956. *Osteology of the reptiles*. University of Chicago Press, Chicago.
- Rosas, A. 1992. Ontogenia y filogenia de la mandíbula en la evolución de los homínidos. Aplicación de un modelo de morfogénesis en las mandíbulas fósiles de Atapuerca. Ph.D. dissertation. Universidad Complutense de Madrid, Madrid.
- Rosen, R. 1991. *Life itself: a comprehensive inquiry into the nature, origin, and fabrication of life*. Columbia University Press, New York.
- Rowe, T. 1986. Homology and evolution of the deep dorsal thigh musculature in birds and other reptilia. *Journal of Morphology* 189:327–346.
- Ruben, J. A., T. D. Jones, N. R. Geist, and W. J. Hillenius. 1997. Lung structure and ventilation in Theropod dinosaurs and early birds. *Science* 278:1267–1270.
- Sanz, J. L., L. M. Chiappe, B. P. Pérez-Moreno, A. D. Buscalioni, J. J. Moratalla, F. Ortega, and F. J. Poyato-Ariza. 1996. An early Cretaceous bird from Spain and its implications for the evolution of avian flight. *Nature* 382:442–445.
- Sereno, P. C. 1991a. Basal archosaurs: phylogenetic relationships and functional implications. *Journal of Vertebrate Paleontology Memoir* (Suppl. to Vol.11, No. 4).
- . 1991b. *Lesothosaurus*, “Fabrosaurids,” and the early evolution of Ornithischia. *Journal of Vertebrate Paleontology* 11: 168–197.
- . 1999. The evolution of dinosaurs. *Science* 284:2137–2147.
- Sereno, P. C., and A. B. Arcucci. 1993. Dinosaurian precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *Journal of Vertebrate Paleontology* 13:385–399.
- . 1994. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. *Journal of Vertebrate Paleontology* 14:53–73.
- Sereno, P. C., and C. H. Rao. 1992. Early evolution of avian flight perching: new evidence from the Lower Cretaceous of China. *Science* 255:845–848.
- Shubin, N., and P. Alberch. 1986. A morphogenetic approach to the origin and basic organization of the tetrapod limb. *Evolutionary Biology* 20:319–387.
- Sommerhoff, G. 1950. *Analytical biology*. Oxford University Press, London.
- Starck, J. M. 1993. Evolution of avian ontogenesis. Pp. 275–366 in D. E. Power, ed. *Current ornithology*, Vol. 10. Plenum, New York.
- Thom, R. [1972] 1977. *Stabilité structurelle et morphogénèse: essai d'une théorie générale des modèles*, 2d ed. InterEditions, Paris.
- Thompson, D'A. W. [1917] 1942. *On growth and form*, new ed. Cambridge University Press, London.
- Waddington, C. H., ed. 1968. *Towards a theoretical biology*. Edinburgh University Press, Edinburgh.
- Walker, A. D. 1977. Evolution of the pelvis in birds and dinosaurs. Pp. 319–357 in S. M. Andrews, R. S. Miles, and A. D. Walker, eds. *Problems in vertebrate evolution*. Academic Press, San Diego.
- Weishampel, D., P. Dodson, and H. Osmólska, eds. 1990. *The Dinosauria*. University of California Press, Berkeley.
- Wellnhofer, P. 1985. Remarks on the digit and pubis problem of *Archaeopteryx*. Pp. 113–122 in M. K. Hecht et al., eds. *The beginnings of birds. Proceedings of the International Archaeopteryx Conference, 1984, Eichstätt*. Freunde des Jura-Museums Eichstätt, Eichstätt.
- . 1991. Additional pterosaur remains from the Santana Formation (Aptian) of the Chapada do Araripe, Brazil. *Palaeontographica* 215:43–101.
- Wimsatt, W. C. 1987. False models as means to truer theories. Pp. 23–55 in M. Nitecki and A. Hoffman, eds. *Neutral models in biology*. Oxford University Press, London.
- Woodger, J. H. 1937. *The axiomatic method in biology*. Cambridge University Press, Cambridge.
- Xu, X., Z. Tang, and X. Wang. 1999. A therizinosauroid dinosaur with integumentary structures from China. *Nature* 399:350–354.