



# The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes)

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Substantial differences in pelvic osteology and soft tissues separate crown group crocodylians (Crocodylia) and birds (Neornithes). A phylogenetic perspective including fossils reveals that these disparities arose in a stepwise pattern along the line to extant birds, with major changes occurring both within and outside Aves. Some character states that preceded the origin of Neornithes are only observable or inferable in extinct taxa. These transitional states are important for recognizing the derived traits of neornithines. Palaeontological and neontological data are vital for reconstructing the sequence of pelvic changes along the line to Neornithes. Soft tissue correlation with osteological structures allows changes in soft tissue anatomy to be traced along a phylogenetic framework, and adds anatomical significance to systematic characters from osteology. Explicitly addressing homologies of bone surfaces reveals many subtleties in pelvic evolution that were previously unrecognized or implicit. I advocate that many anatomical features often treated as independent characters should be interpreted as different character states of the same character. Relatively few pelvic character states are unique to Neornithes. Indeed, many features evolved quite early along the line to Neornithes, blurring the distinction between 'avian' and 'non-avian' anatomy.

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ADDITIONAL KEYWORDS: Archosauria – crocodile – dinosaur – Aves – homology – character evolution – pelvis – ligament – muscle.

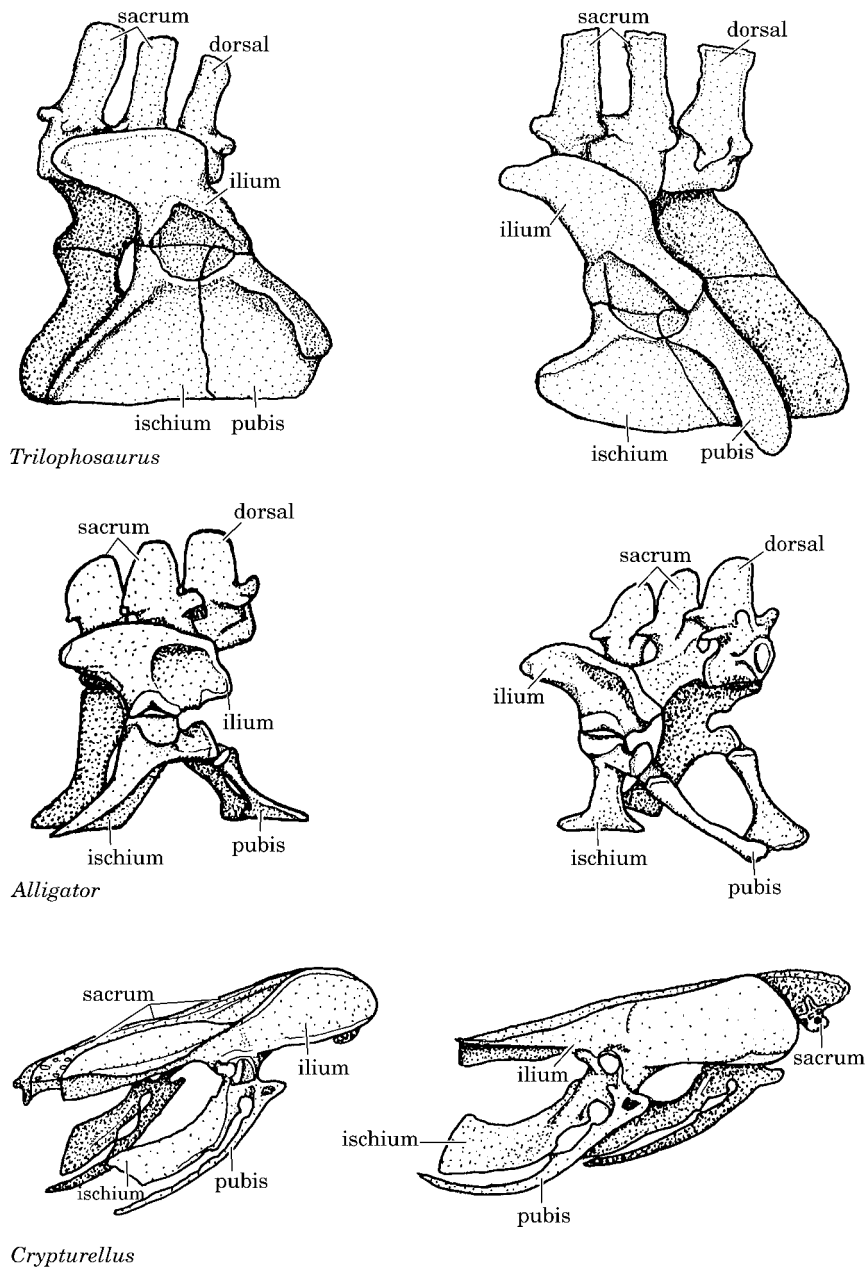
## INTRODUCTION

Crown group crocodylian (Crocodylia) and bird (Neornithes) pelves share some derived morphological characteristics that are synapomorphies at some level within the clade Archosauromorpha (*sensu* Gauthier, Klug & Rowe, 1988). However, many aspects of these bones differ strikingly between these two clades of extant Archosauria, making some comparisons difficult. For example, compared to crocodylians or basal archosauromorphs (Fig. 1), the neornithine pelvis ancestrally has a greatly expanded ilium as well as pubes and ischia that are retroverted, highly elongated, and widely separated from their contralateral elements. These differences become even more obvious when soft tissues, including muscles, membranes, and ligaments, are also considered (Romer, 1923a,b,c, 1927a; Parrish, 1983; Gatesy, 1990; McKittrick, 1991). The similarities and differences among extant archosaur pelves are

more easily understood in a phylogenetic context that includes extinct archosauromorphs, which are important outgroups for calibrating character state polarity (Maddison, Donoghue & Maddison, 1984; Gauthier *et al.*, 1988; Maddison & Maddison, 1992).

Considerable changes of posture, limb orientation, kinematics, and other parameters accompanied these morphological changes as archosauromorphs diversified (Romer, 1923a,b,c; Colbert, 1964; Charig, 1972; Walker, 1977; Tarsitano, 1983; Parrish, 1986; Gatesy, 1990, 1991, 1995, in press; Sereno, 1991a; Gatesy & Dial, 1996; Novas, 1996; Chatterjee, 1997; Carrano, 1998; Reilly & Elias, 1998). Changes in thigh musculature associated with the evolution of erect posture, bipedalism, perching and climbing, and parasagittal gait have received particular attention (e.g. Romer, 1923a; Charig, 1972; Parrish, 1986; Proctor & Lynch, 1993), as have changes in pelvic musculature associated with lung ventilation (Carrier & Farmer, 2000). Pelvic soft tissues are vital for body support and locomotor function, but the biological role (e.g. significance for soft tissues, or functional morphology)

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**Figure 1.** Pelves of *Trilophosaurus* (basal Archosauromorpha; left pelvis of AMNH 7502, reversed), *Alligator* (Crocodylia; UCMP 131080), and *Crypturellus* (Neornithes; MVZ 85503), in caudolateral view (on left) and craniolateral view (on right). The three pelvic bones (ilium, ischium, and pubis) are labelled, as are the sacral vertebrae and the last dorsal vertebra. Not to scale.

of many systematic characters from pelvic osteology is unknown.

I adopt a broad phylogenetic perspective to analyse the sequence of anatomical evolution of archosauromorph pelves. My major question is: How did the neornithine pelvis acquire its modern character

states? In other, words, when did specializations of the neornithine pelvis evolve, or what clades are these features synapomorphies for? I also address the implications for soft tissue evolution of some osteological traits that are often used as systematic characters. I do not cover all aspects of osteological and soft tissue

anatomy; I will address the evolution of the hip joint, femur, and thigh muscles in more detail in future studies. I focus on the line to crown group birds (also see Gatesy, in press): the lineage of descent from basal Archosauromorpha through ancestral nodes to Neornithes (extant birds following Cracraft, 1986; Chiappe, 1996; Padian, Hutchinson & Holtz, 1999; equivalent to *Aves sensu* Gauthier, 1986).

My study is of interest to biologists in general because it integrates a wealth of data from osteology, myology, and phylogeny to reconstruct the evolution of the archosauromorph pelvis, a complex anatomical region whose history remains poorly understood. My approach is generalizable to other major transitions such as the evolution of mammalian limbs or the avian pectoral complex. My conclusions are complementary to those of other researchers such as Carrier and Farmer (2000), and can aid in interpreting unusual fossils (e.g. Martill *et al.*, 2000). Many previous analyses of the archosaur pelvis have lacked a phylogenetic context, used only a few taxa or specimens, and used inaccurate data on bone and soft tissue anatomy. This analysis establishes some basic comparisons among disparate archosauromorph and non-archosauromorph taxa and forms the foundation for further studies of sauropsid hindlimb evolution. I resolve some issues of pelvic evolution, including bone structure and bone surface homologies, thigh muscle evolution, and the homologies and evolution of the pelvic membranes and ligaments. These data are indispensable for reconstructing how archosaur locomotion evolved.

## ABBREVIATIONS

### INSTITUTIONAL ABBREVIATIONS

I examined specimens from the following institutions during the course of my study: AMNH, American Museum of Natural History, New York, New York; BYU, Brigham Young University Geological Museum, Provo, Utah; CAS, California Academy of Sciences, San Francisco, California; CM, Carnegie Museum, Pittsburgh, Pennsylvania; CMNH, Cleveland Museum of Natural History, Ohio; DMNH, Denver Museum of Natural History, Colorado; FMNH, Field Museum of Natural History, Chicago, Illinois; IGM, Geological Institute of Mongolia, Ulan Bataar, Mongolia; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MUCPv, Museo de Ciencias Naturales, Universidad Nacional del Comahue, Neuquén, Argentina; MVZ, University of California Museum of Vertebrate Zoology, Berkeley, California; NGMC, National Geological Museum of China, Beijing, People's Republic of China; NMMNH, New Mexico Museum of Natural History, Albuquerque, New Mexico; PVL, Fundación 'Miguel Lillo', San Miguel de Tucumán, Argentina; PVSJ, Museo de Ciencias

Naturales, Universidad Nacional de San Juan, San Juan, Argentina; ROM, Royal Ontario Museum, Toronto, Ontario; TMM, Texas Memorial Museum, Austin, Texas; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; TTUP, Texas Tech University Museum, Lubbock, Texas; UA, Université d'Antananarivo, Madagascar; UCMP, University of California Museum of Paleontology, Berkeley, California; UCOBA, University of Chicago Department of Organismal Biology and Anatomy, Chicago, Illinois (temporary listing); USNM, Museum of Natural History, Smithsonian Institution, Washington (D.C.); UUVP, Utah Museum of Natural History, Salt Lake City, Utah; YPM, Yale Peabody Museum, New Haven, Connecticut.

### ANATOMICAL ABBREVIATIONS

bf	brevis fossa	of	obturator foramen
cf	preacetabular fossa	on	obturator notch
ci	crista infracristalis	op	obturator process
cps	cranio-lateral pubic symphysis	ot	obturator tuberosity
dep	depression for the ADD2 origin	pa	pubic apron
fid	fossa iliaca dorsalis	pb	pubic boot
ib	ischial boot	pc	pelvic canal
iif	ilio-ischiadic fenestra	pdp	proximal dorsal ischial process
ir	ischial ridge	pf	pubic foramen
it	ischial tuberosity	ps	processus supratrochantericus
		pt	pubic tubercle

For muscle abbreviations see Table 1.

## MATERIAL AND METHODS

I examined extant and fossil specimens of a broad range of archosauromorph taxa in order to collect osteological data. I dissected nine specimens of *Alligator mississippiensis* and many neornithine birds for soft tissue data, in addition to one specimen of *Sphenodon* (CAS 208882) as well as numerous squamates and chelonians for outgroup comparison. Table 1 lists the muscle homologies (and their abbreviations) used herein. Table 2 and Figure 2 show the soft tissue attachments for representative extant Reptilia (based on my dissections and Gadow, 1882a,b, 1891; Romer, 1922, 1923b; McKittrick, 1991). I adopt Romer's (1923b, 1942) muscle homologies, with Rowe's (1986) revision of deep dorsal thigh muscle homologies. Anatomical nomenclature for Aves follows Baumel *et al.* (1993), but more familiar English names for some structures are used. Non-avian reptilian anatomical nomenclature follows Romer (1922, 1923b, 1956) and similar traditional nomenclature. All figures depict

**Table 1.** Muscle homologies for Reptilia, following Romer (1922, 1923a, 1927b, 1942) and Rowe (1986), with abbreviations used in this study. Not all thigh muscle groups are listed. 'ND' indicates that the muscle is not divided; '—' indicates that the muscle is absent. See Figs 2, 14, 16, and 19 for illustrations

	Chelonia	<i>Sphenodon</i>	Squamata	Crocodylia	Neornithes
DORSAL GROUP					
1. Triceps femoris					
(a) M. iliotibialis	IT	IT	IT	IT	IT
(b) M. ambiens	AMB	AMB	AMB	AMB1+2	AMB
2. M. iliofibularis	ILFB	ILFB	ILFB	ILFB	ILFB
3. Deep dorsals					
(a) M. iliofemoralis	IF	IF	IF	IF	IFE
	ND	ND	ND	ND	ITC
(b) M. pubo-ischio-femoralis internus					
	PIFI1+2	PIFI1+2	PIFI1	PIFI1	IFI
	ND	ND	PIFI2	ND	ND
	PIFI3	PIFI3	PIFI3	PIFI2	ITCR
	ND	ND	ND	ND	ITM
VENTRAL GROUP					
4. Flexor cruris					
(a) M. pubo-ischio-tibialis					
	PIT	PIT	PIT1	—	—
	ND	ND	PIT2	PIT	—
	ND	ND	PIT3	FTI2	—
(b) M. flexor tibialis internus					
	FTI1	FTI1	FTI1	FTI1	—
	FTI2	FTI2	FTI2	FTI3+4	FCM
(c) M. flexor tibialis externus					
	FTE	FTE	FTE	FTE	FCLP
5. M. pubotibialis	PUT	PUT	PUT	—	—
6. M. adductor femoris	ADD	ADD	ADD	ADD1	PIFM
	ND	ND	ND	ADD2	PIFL
7. M. pubo-ischio-femoralis externus					
	PIFE	PIFE	PIFE	PIFE1	OL
	ND	ND	ND	PIFE2	OM
	ND	ND	ND	PIFE3	—
8. M. ischiotrochantericus	ISTR	ISTR	ISTR	ISTR	ISF
9. M. caudofemoralis brevis	CFB	CFB	CFB	CFB	CFP

elements from the right side of the body in lateral view unless otherwise noted.

I coded and scored pelvic characters into a data matrix (Appendix 2) and visualized character state transformations using MacClade 3.08 (Maddison & Maddison, 1992), summarized in Appendix 3. My minor modifications of archosauromorph homologies will not introduce 'inappropriate bias' (*sensu* de Queiroz, 1996) by modifying the underlying phylogenetic framework. This is because any weakly supported or unresolved nodes are collapsed, and only well supported clades are used. 'Support' is gauged by my judgement of consensus in the systematic literature. However, the nodes in my tree are not solely supported by the pelvic characters that I use. Indeed, several of my characters have never been used in cladistic analyses, but would be unlikely to alter archosaur phylogeny if included.

#### PHYLOGENY

I use a conservative 'consensus' phylogenetic framework (Fig. 3) for character analysis (see Appendices). By 'consensus' I mean that I have collapsed nodes that I consider controversial based on published analyses. This is a subjective estimate of consensus; I do not reanalyse all of archosauromorph phylogeny and compute an actual consensus tree. The phylogeny is based on Gauthier (1986), Benton & Clark (1988), Gauthier *et al.* (1988), Sereno & Arcucci (1990), Sereno (1991a), Parrish (1993), Juul (1994), Gower & Wilkinson (1996), and Dilkes (1998) for non-ornithodiran Archosauromorpha. I use the crown group nomenclature for Reptilia and Archosauria endorsed by Gauthier *et al.* (1988), but use the names Aves (for all birds) and Neornithes (for extant birds) *sensu* Padian *et al.* (1999).

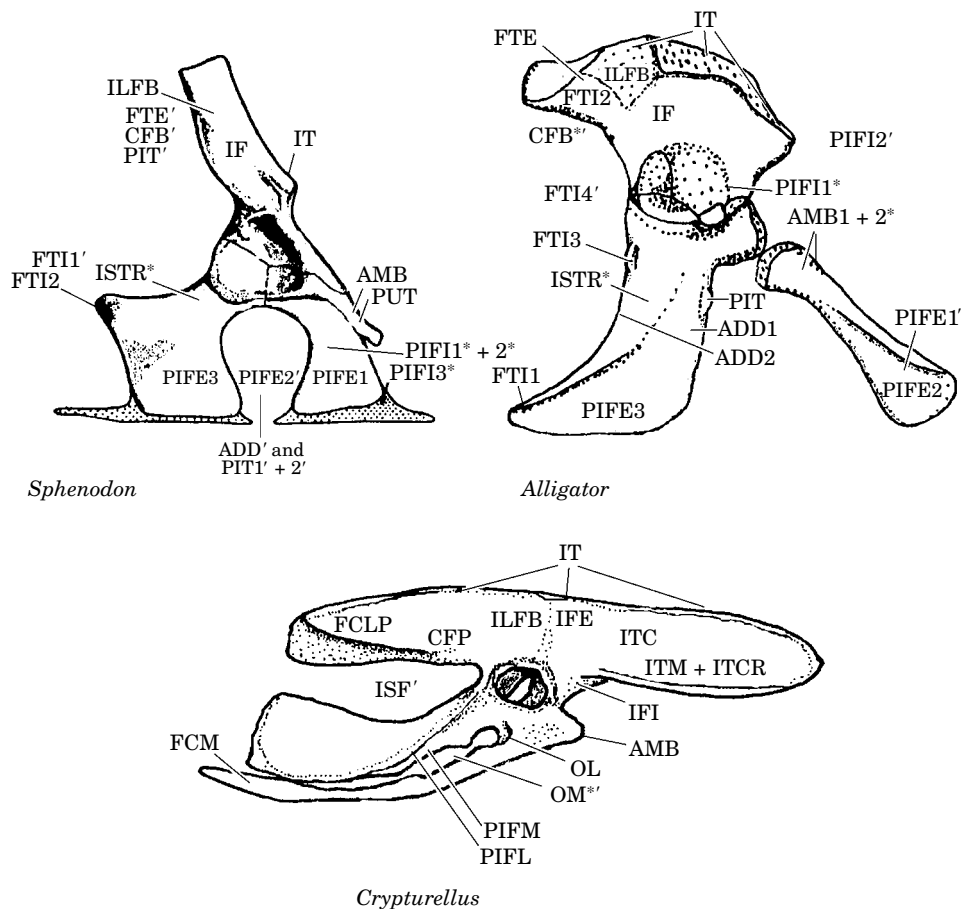
**Table 2.** Osteological correlates of pelvic soft tissue attachments in extant Reptilia

Structure/Surface	Basal Reptilia	Crocodylia	Neornithes
<b>PREACETABULAR ILIUM</b>			
Lateral surface	IT	IT	IT, ITC + IFE, ITM + ITCR
Medial surface	M. dorsalis trunci	M. dorsalis trunci, PIFI1	M. dorsalis trunci
Ilio-pubic ligament	Mm. obliqui abdomini	(strongly reduced)	Mm. obliqui abdomini
<b>POSTACETABULAR ILIUM</b>			
Lateral surface	IT, IF, ILFB, FTE	IT, IF, ILFB, CFB, FTE, FTI2	IT, IF, ILFB, CFB, FCLP
Medial surface	M. dorsalis caudae, CFB	M. dorsalis caudae, CFB	M. dorsalis caudae
Ilio-ischiadic ligament/ membrane	FTI1, PIT3	(reduced). FTI 4	ISF
<b>PUBIS</b>			
Pubic tubercle	AMB, PUT, pelvic ligaments, hypaxial muscles	(reduced)	AMB, pelvic ligaments, hypaxial muscles
<b>PUBIC SYMPHYSIS</b>			
Cranial surface	PIFI3	PIFE1	(absent)
Caudal surface	PIFE	PIFE2	(absent)
<b>PUBIC SHAFT</b>			
Lateral surface	hypaxial muscles	hypaxial muscles	hypaxial muscles, OL
Pubo-ischiadic ligament	PIT1 + 2, ADD	(reduced)	(reduced)
Pubo-ischiadic membrane	PIFE (lateral), PIFI1 + 2 (medial)	(nothing)	OM (medial)
<b>ISCHIUM</b>			
Ischial tuberosity	pelvic ligaments, FTI2	fascia, pubo-ischiadic ligament, FTI3	ilio-ischiadic membrane
<b>ISCHIAL SHAFT</b>			
Lateral surface	PIFE	PIFE3, ADD1 + 2, PIT, FTI1	FCM, PIFM + PIFL, ISF
Medial surface	PIFI1 + 2, ISTR	PIFI1, ISTR	caudal musculature

For non-ornithodiran Archosauriformes, I primarily use the reduced consensus tree presented by Gower & Wilkinson (1996). The arrangement of *Doswellia*, *Euparkeria*, and Proterochampsidae outside Archosauria is unresolved, and Ornithosuchidae is left in a trichotomy with other Crurotarsi. The relationships of Rauisuchidae and Poposauridae to Crocodylomorpha are also uncertain. Crocodylomorpha is simplified as three subsets of taxa: paraphyletic basal Crocodylomorpha and basal Crocodyliformes, and monophyletic (crown group) Crocodylia (following Russell & Wu, 1997; and references therein).

Ornithodiran, especially theropod, phylogeny and taxonomy is based on Gauthier (1986), Novas (1994, 1996, 1997), Holtz (1994, in press), Chiappe (1996), Chiappe, Norell & Clark (1996), Sereno (1999), Forster *et al.* (1998), and Padian *et al.* (1999). Neotheropoda

has several controversial nodes: basal Neotheropoda (Coelophysoidea and Ceratosauria) and Maniraptoriformes (Tyrannosauridae, Troodontidae, and Ornithomimosauria) are grouped as polytomies. Tetanurae is grouped as 'basal Tetanurae 1' (e.g. Spinosauridae and Torvosauridae), 'basal Tetanurae 2' (e.g. *Afrovenator* and *Piatnitzkysaurus*), and Averotheropoda (= Neotetanurae of Sereno, 1999). 'Basal Coelurosauria' includes taxa such as Compsognathidae, *Deltadromeus*, *Gasosaurus*, *Ornitholestes*, and *Scipionyx* (Sereno, 1999; Holtz, 2000). The relationship of the basal Avialae *Rahonavis* and *Unenlagia* to *Archaeopteryx* and other Aves is left unresolved. In referring to Neornithes, I address the ancestral condition for crown group birds (based on Cracraft, 1986; McKittrick, 1991; Chiappe, 1996; and pers. observ.) rather than variation within the clade.



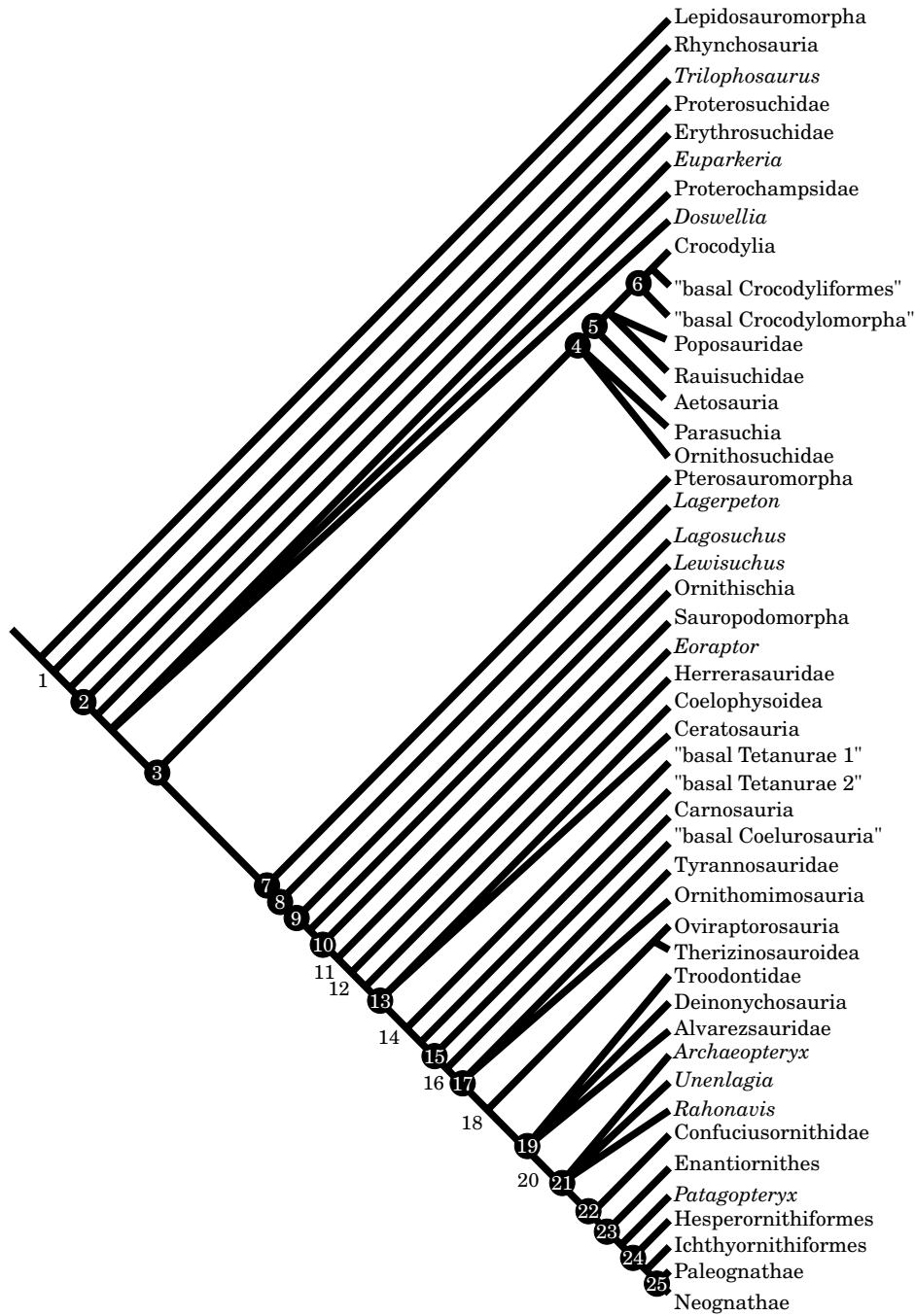
**Figure 2.** Pelvic myology of extant Reptilia, represented here by *Sphenodon* (Lepidosauria; modified from Romer, 1956), *Alligator* (Crocodylia; UCMP 138037), and *Crypturellus* (Neornithes; MVZ 85503). Based on my dissections. Abbreviations are in Table 1. Abbreviations ending in an apostrophe (') originate mainly from nearby fascia, ligaments, and/or vertebrae. Abbreviations ending in an asterisk (\*) originate medial to the point indicated (i.e. behind the surface shown). Not to scale.

#### HOMOLOGY

The definition of homology that I use here is equivalent to synapomorphy (and symplesiomorphy) following Patterson (1982), Rieppel (1994), and Roth's (1994) 'supra-specific homology'. As Patterson (1982) noted, it is important to specify the nature of homology (e.g. character vs. character state, ancestral vs. derived) proposed. The tests of similarity, conjunction, and congruence are necessary for proposing and testing homology propositions. The test of similarity is the most subjective of these tests (de Pinna, 1991; Brower & Schawaroch, 1996; Hawkins, Hughes & Scotland, 1997). This subjectivity does not eliminate the value of the test of similarity to morphologists, but warrants caution in its application. Overemphasizing similarity can lead to essentialism; phylogenetic congruence is of paramount importance for testing hypotheses of homology (Patterson, 1982; de Pinna, 1991; Rieppel, 1994; Roth, 1994). How-

ever, I do not see homology as solely a taxic concept. I seek to emphasize both taxic and transformational perspectives on homology (also see McKittrick, 1991; Carine & Scotland, 1999; Kluge & Farris, 1999).

Some features of the archosauromorph pelvis are more parsimoniously interpreted as separate character states rather than as distinct, independent characters (for the distinction between characters and their states see Patterson, 1982; Pleijel, 1995; Hawkins *et al.*, 1997). This is similar to the 'splitting vs. lumping' controversy in systematics. Such problems in character state coding are sometimes overlooked when character analyses do not consider a broad range of outgroup taxa in detail. These problems are especially prevalent when subjective assessments of 'similarity' supersede overwhelming evidence from character congruence or ignore problems with character state conjunction (Patterson, 1982).



**Figure 3.** ‘Consensus’ phylogenetic framework used for character mapping in this study. Node-based taxa are labelled at nodes, whereas stem-based taxa are along the stems; see Gauthier *et al.* (1988), Padian *et al.* (1999), and Sereno (1999). Numbers correspond to these taxa (node-based taxa in bold type): 1, Archosauromorpha; 2, Archosauriformes; 3, Archosauria; 4, Crurotarsi; 5, Suchia; 6, Crocodylomorpha; 7, Ornithodira; 8, Dinosauriformes; 9, Dinosauria; 10, Saurischia; 11, Theropoda; 12, Neotheropoda; 13, Tetanurae; 14, Avetheropoda; 15, Coelurosauria; 16, Maniraptoriformes; 17, Maniraptora; 18, Eumaniraptora; 19, Avialae; 20, Aves; 21, Pygostylia; 22, Ornithothoraces; 23, Ornithurae; 24, Neornithes.

Essentialism is frequently cited as a persistent problem in systematics. Essentialistic concepts of morphological characters (and functions) are at least as pervasive as essentialistic concepts of taxa. I suggest that this results from an overemphasis on taxic homology and an underemphasis on transformational homology, *sensu* Patterson (1982: 43), who criticized transformational homology as 'vacuous'. Both perspectives are vital, not vacuous, if comparative anatomical studies are to avoid an overdose of essentialism, or worse yet, become non-evolutionary (also see Roth, 1994; Hawkins *et al.*, 1997). Essentialism is a useful heuristic abstraction (Rieppel, 1994), but its influence on our view of biological reality can be tenacious and obfuscatory.

I use an approach that I feel is unfortunately not often taken during character analysis: emphasizing transformational homology by 'lumping' several characters as multistate. I recognize that this is often a matter of opinion rather than straightforward methodology. Nonetheless, I stress the importance of explicit character analysis. Subjectivity is a problem for both the 'splitting' and 'lumping' approaches to character coding; it is just often more implicit in the former approach. Hypotheses of morphological homology compare structures that are similar enough to recognize them as having a common ancestry (the taxic element of homology; 'primary homology' of de Pinna, 1991), but different enough to accept their divergence from this common ancestry because of overall phylogenetic congruence (the transformational element of homology; 'secondary homology' of de Pinna, 1991). I present many examples here that illustrate this point.

I use 'bone surface homology' to refer to the correspondence of osteological regions that results from common ancestry. Bone surfaces are general regions (e.g. the cranial surface of the pubis) rather than specific, discrete structures of regions (e.g. the pubic tubercle). The distinction between structures and surfaces is often arbitrary but it is useful for this study. Bone surfaces are connected through evolution by continuity of information (*sensu* Roth, 1994). For example, the 'dorsal' bone surface of the femur of a sprawling basal reptile corresponds to the 'lateral' bone surface of a highly adducted bird femur. The medial surface of the neornithine femoral head is a bone surface that ancestrally faced cranially but was inflected medially to form the offset femoral head (Carrano, in press). This view of osteological homology explicitly removes confusion that may arise from changes in bone orientation or frame of reference (e.g. a lateral view of the hindquarters of a crocodylian and neornithine includes different bone surfaces, not all of which are historically lateral surfaces). It is not a novel perspective, but it is unfortunately often implicit rather than explicit in many comparative anatomical studies.

#### SOFT TISSUE INFERENCES

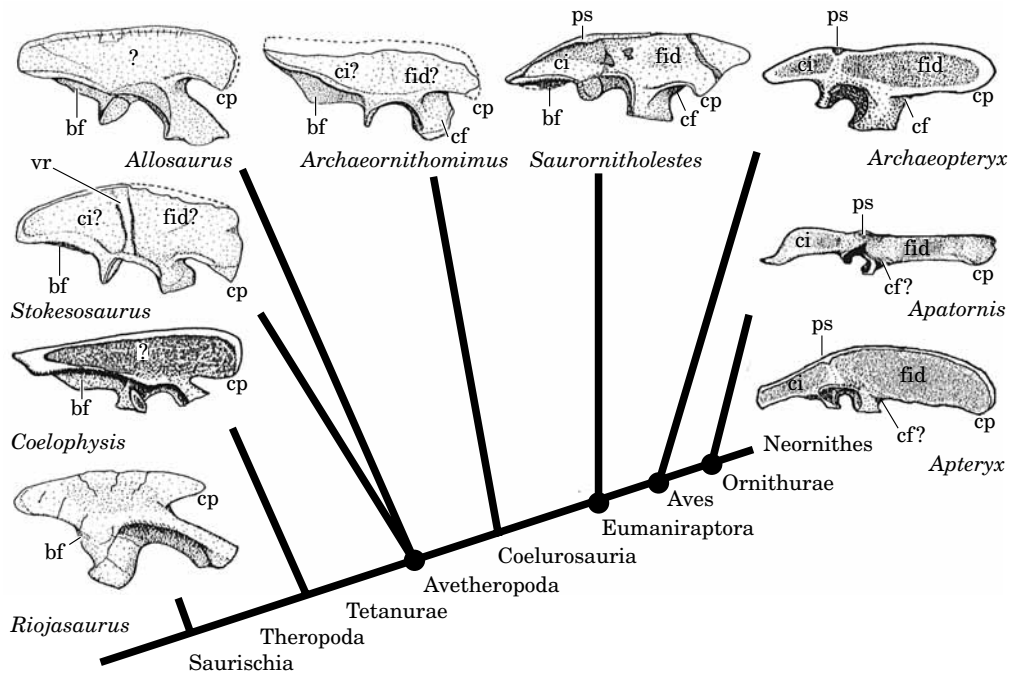
In analysing soft tissue evolution I use an approach similar to the paradigms outlined by Bryant & Russell (1992) and Witmer's (1995) 'extant phylogenetic bracket'. Osteological correlates of soft tissue attachment in extant taxa are optimized by the outgroup method (Maddison *et al.*, 1984) on a phylogenetic framework that includes fossils. If osteological correlates pass the test of congruence then their associated soft tissues are also considered homologous. 'Congruence' is with my phylogenetic framework and not with the character states that support the tree (as many systematists would favour). I do not have space here to reanalyse the hundreds of characters used in archosauromorph phylogeny, but the distinction between tree congruence and character congruence should make little if any difference for my conclusions on character homologies.

There are difficulties in interpreting muscle scars and other osteological correlates in fossils (also see McGowan, 1979; Bryant & Seymour, 1990; Bryant & Russell, 1992; Witmer, 1995, 1997). One problem is that the connections between bony features and associated soft tissues need not evolve in lockstep fashion. The fourth trochanter of the femur of archosaurs ancestrally was the insertion of *M. caudofemoralis longus* (Gatesy, 1990), but the trochanter was strongly reduced (or 'lost') in maniraptoran theropods. However, the reduced muscle remains in many living birds (Gadow, 1891; McKittrick, 1991) and in more basal Maniraptora (Gatesy, 1995; Norell & Makovicky, 1999), often without attaching to a visible fourth trochanter. Therefore, the 'loss' of osteological correlates need not coincide with the loss of their associated soft tissues.

Furthermore, connections among soft tissues and their bony attachments are not always simple one-to-one relationships. They are often complex, with more than one soft tissue attaching to a bony structure (e.g. the pubic tubercle, discussed below). In many cases several alternative possibilities for soft tissue attachment at a bone surface must be falsified before a single attachment can be inferred safely (e.g. muscle origins on the pubis, discussed below). Unlike tendinous attachments, fleshy muscle attachments seldom leave discrete scars (McGowan, 1979; Bryant & Seymour, 1990), but intermuscular lines may separate them from other soft tissues (e.g. the iliac concavities and ischial ridge discussed below). Not all osteological modifications are for muscle attachment, either.

Taphonomic, ontogenetic, and allometric variation also must be considered when interpreting muscle scars. Muscle scars are not always preserved and can be easily abraded from bones. Osteological correlates are less obvious in smaller and/or younger specimens, although especially large taxa (e.g. saurpods) may also secondarily reduce muscle scarring. Nonetheless,





**Figure 4.** Evolution of the ilium on the line to Neornithes. Iliia include *Riojasaurus* (PVL 3667), *Coelophysis* (modified from Rowe & Gauthier, 1990), *Stokesosaurus* (left ilium of UUVF 2938, reversed), *Allosaurus* (left ilium of MOR 693, reversed), *Archaeornithomimus* (left ilium of AMNH 21790, reversed), *Saurornitholestes* (MOR 660), *Archaeopteryx* (modified from Chatterjee, 1997), *Apatornis* (modified from Marsh, 1880), and *Apteryx* (modified from McGowan, 1979). '?' indicates that division of the ilium into preacetabular and postacetabular concavities (i.e. 'fid' and 'ci') is uncertain. 'vr' is the median vertical ridge. Scaled to the same ilium length.

I have observed remarkable consistency among muscle scars of extant taxa. Some scars are present even in young (e.g. embryonic or juvenile Crocodylia and Neornithes that I have examined) or pathological individuals. For example, an osteoporotic specimen of *Caiman* (UCMP 123095) has all of the osteological correlates that I have seen in other crocodylians, even though many of its bones are badly eroded.

PELVIC EVOLUTION

ILIAC STRUCTURES

Bone surface homologies for the ilium are straightforward because the ilium is mediolaterally compressed and mainly comprises medial and lateral surfaces (the cranial and caudal edges are very thin; Figs 1, 5). The most prevalent changes of the archosauriform ilium were shape changes such as craniocaudal and dorsoventral expansion (Colbert, 1964; Charig, 1972; Parrish, 1983, 1986; Carrano, 2000), especially within Theropoda (Fig. 4). Some iliac structures, such as the acetabulum and sacral rib attachments, form useful reference points. Craniocaudal expansion of the iliac blade is generally correlated with increasing sacral vertebral count,

especially within pterosaurs and dinosaurs (including birds). Expansions of the preacetabular and/or postacetabular ilium can be roughly gauged by increases in sacral vertebral count from the ancestral two vertebrae, although as Novas (1996) noted, shortening of sacral vertebrae is also involved in increasing sacral vertebral count.

Sacral and iliac evolution

On the line to Neornithes, archosauriforms evolved an expanded cranial process of the ilium (Figs 4, 8: cp). In Dinosauria, the addition of one vertebra from the dorsal vertebrae to the sacrum (Gauthier, 1986; Novas, 1996; but see Galton, 1999 for an alternative view) was associated with a cranial expansion of the preacetabular ilium. Neotheropoda added another dorsal and one caudal vertebra as the ilium became more dolichoiliac (*sensu* Colbert, 1964). Many non-avian maniraptoriforms added another dorsal vertebra to the sacrum (Chiappe, 1996; Sereno, 1999; Holtz, in press), totalling six or more sacral vertebrae. It is not well understood which vertebrae were added to the avian synsacrum. Confuciusornithidae added a seventh vertebra (Martin *et al.*, 1998; Ji, Chiappe & Ji, 1999), Ornithothoraces brought the sacral count

to at least eight, Ornithurae ancestrally had 10, and Neornithes has 11–23 (Chiappe, 1996). This is consistent with a protracted pattern of expansion of the ilium (especially cranially) from basal Archosauromorpha to Neornithes (also see Chatterjee, 1997: 213).

Cranial expansion of the preacetabular ilium would have moved the centroids of the deep dorsal thigh muscle (and *M. iliotibialis*) origins cranially. This would have increased their physiological cross sectional areas and hence increased force production, as well as increased their moment arms for protraction (Colbert, 1964; Charig, 1972; Parrish, 1986; Carrano, 2000) and medial femoral rotation.

Biomechanical or functional implications of increased sacral vertebral count are not clear, although an expanded sacrum clearly reduces the mobility of vertebrae that were ancestrally outside the sacrum. The sacrum incorporated two extra vertebrae (totalling at least five) within Pterosauriforms, Ornithischia, and Neotheropoda, all of which are ancestrally quite small animals. Consequently, adding vertebrae to the sacrum is not necessarily always a size-related pattern. The small size of basal avians, which have expanded synsacra, further complicates this pattern, and large theropods (e.g. carnosaurs and tyrannosaurs) do not always increase sacral vertebral count either. Few if any taxa reduced sacral vertebral count; Herrerasauridae is one possibility.

#### *Iliac surfaces*

The preacetabular surface of the avian ilium is termed the *ala preacetabularis ilii* (Baumel & Witmer, 1993). It is often twisted dorsally in neognaths, but it is the bone surface homologous with the short preacetabular ilium of other Reptilia (Figs 4, 5). In birds and other archosaurs it generally remains narrower than the postacetabular ilium (except in some aetosaurs, sauropodomorphs, therizinosauroids, and other taxa). Its concave lateral surface (the *fossa iliaca dorsalis* of Aves; Figs 4, 5: fid) is part of the origin of the deep dorsal thigh muscles in all Reptilia (Fig. 2). The convex, rugose dorsal rim of the preacetabular ilium (the *crista dorsalis ilii* of Aves; Fig. 5: cd) is ancestrally the origin of the preacetabular part(s) of *M. iliotibialis*. More medially it is the attachment for epaxial musculature (e.g. *M. dorsalis trunci*).

The postacetabular surface of the avian ilium is called the *ala postacetabularis ilii*. It is the bone surface equivalent to the long postacetabular ilium of other Reptilia. Unlike the preacetabular ilium, it is generally widened in birds. In Aves, it consists of two parts that correspond to the *fossa iliaca dorsalis* and the *crista dorsalis ilii* of the preacetabular ilium. These parts are respectively called the *concauitas infracristalis* (the

postacetabular iliac concavity; Fig. 2B: ci) and the *crista dorsolateralis ilii* (Fig. 5: cdl). The avian *concauitas infracristalis* (or *lamina infracristalis ilii*) is the bone surface homologous with the lateral surface of the postacetabular ilium in non-avian Reptilia (Figs 4, 5). *M. iliofibularis*, parts of the flexor cruris group, and other thigh muscles originate from the lateral iliac surface in all Reptilia (Fig. 2; Table 2).

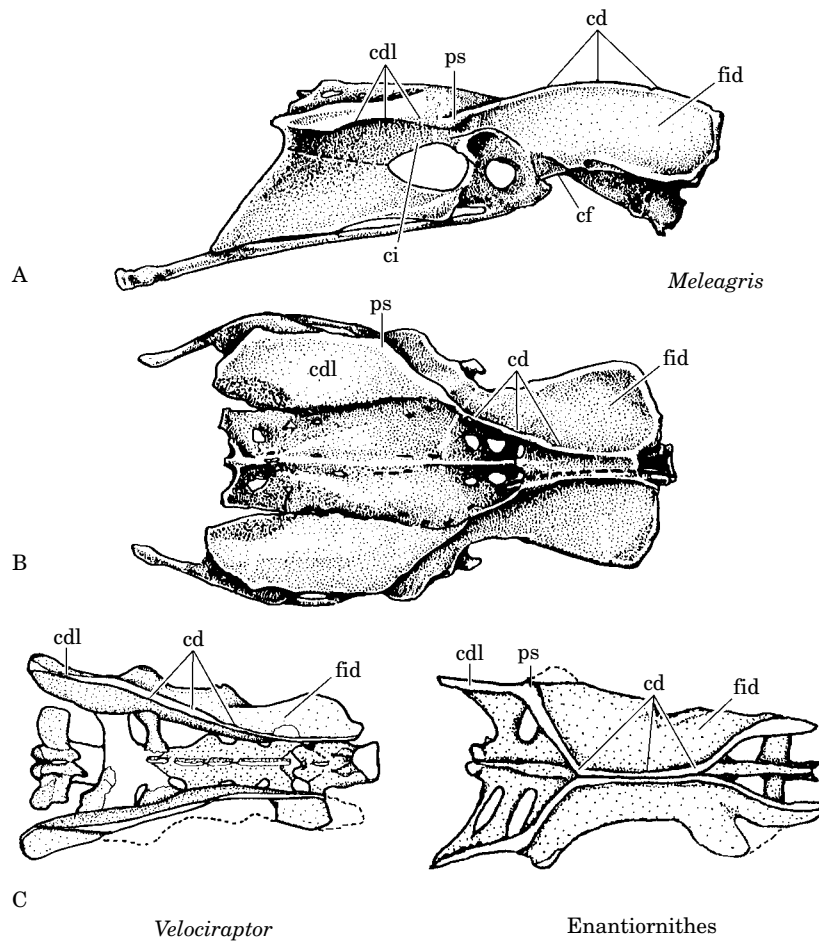
The avian *crista dorsolateralis ilii* is a transverse expansion of the dorsal iliac rim, serving as the origin for the remainder of *M. iliotibialis* as well as epaxial muscles (e.g. *M. levator caudae*; = *M. dorsalis caudae* of basal Reptilia). Accordingly, it is not homologous with the lateral bone surface of the postacetabular ilium of other Reptilia (as it might appear to be from illustrations), but rather with the dorsal (and possibly medial) rim of the iliac blade. The *crista dorsolateralis ilii*, including its ventrolateral process (the *processus supratrochantericus*; Fierbas & Zweymüller, 1971; see below), became increasingly prominent in basal birds as the postacetabular region and the synsacrum widened. The fusion of the sacral ribs into a dorsal lamina medial to the dorsal iliac rim, often prominent in Neognathae, is another change correlated with widening the synsacrum.

The right and left iliac blades became more closely appressed in many coelurosaurs (Holtz, 1994; Sereno, 1999), especially cranially (Fig. 5). Perhaps this change was associated with the segregation of the epaxial musculature into fully independent *M. dorsalis trunci* and *M. levator* (= *dorsalis caudae*) portions. The homologues of these muscles were ancestrally more continuous but are well separated craniocaudally in Neornithes. This is another line of evidence suggesting that the tail became progressively more decoupled from the rest of the body within Coelurosauria, especially in birds (Gatesy & Dial, 1996).

#### *Iliac subdivision*

The dorsal rim of the ilium expanded ventrolaterally in some taxa to form structures such as the *processus supratrochantericus* of some theropods and the 'antitrochanter' (*sensu* Romer, 1927a) of some ornithischians. These projections are ventrolateral expansions of the dorsal iliac rim, not articular surfaces. They are dorsal to the acetabular antitrochanter but may be connected to it by a subvertical ridge. Such structures span the border between the preacetabular and postacetabular iliac concavities (and their associated thigh muscle origins), forming another comparative reference point.

The *processus supratrochantericus* (Figs 4, 5: ps) of Eumaniraptora marks the caudal border of the preacetabular ilium (including the origin of *M. iliofemoralis externus*) and the cranial border of the post-



**Figure 5.** Features of the maniraptoran sacrum and ilium. A and B, *Meleagris* (Neognathae; modified from Baumel & Witmer, 1993) in lateral view (in A) and dorsal view (in B). C, *Velociraptor* (Deinonychosauria; IGM 100/985) and an enantiornithine (Ornithothoraces; PVL 4041-4) in dorsal view. 'cd' is the crista dorsalis ilii (preacetabular iliac crest), and 'cdl' is the crista dorsolateralis ilii (postacetabular iliac crest), which expands laterally in birds, especially neognaths. Scale bar = 1 cm.

acetabular ilium (including the origin of *M. iliofibularis*). Thus the processus supratrochantericus and the division of the ilium into two main concavities are ancestral features for Eumaniraptora (Table 3A). The postacetabular ilium is smaller than the preacetabular ilium in these taxa, and remains small in many Eumaniraptora. This may be part of a more complex pattern of pelvic membrane formation and the widening of the hips (see Pelvic Membranes, pp. 154–156).

Some non-eumaniraptoran Theropoda (Table 3A) have vertical supra-acetabular iliac ridges (Fig. 4: vr) that suggest some division of the ilium into separate concavities, as in Eumaniraptora. However, these features do not currently optimize as tetanuran plesiomorphies (i.e. they do not pass the test of congruence). Because the origins of most of the lateral

iliac muscles are fleshy and do not commonly leave clear evidence of their boundaries, the extents of their origins are difficult to infer (Fig. 4). It is difficult to test whether *M. iliofemoralis* (IF) was split into two heads in these taxa (Romer, 1923a,c; Russell, 1972), whether the ridge marks a boundary between the IF and *M. iliofibularis* (Walker, 1977), or whether the coelophysid iliac fossa for the IF noted by Rowe & Gauthier (1990) was occupied only by that muscle. Further study should clarify how and when iliac subdivision evolved, and what its broader significance was.

Neornithes ancestrally has two heads of the IF muscle group: a small *M. iliofemoralis* externus and a large *M. iliotrochantericus* caudalis (Fig. 1; Rowe, 1986; McKittrick, 1991). Unfortunately, iliac morphology does not unequivocally clarify when this muscle division

**Table 3.** Taxonomic distribution of some iliac features discussed in the text

A1. Presence of the processus supratrochantericus on the ilium (Figs 4, 5: ps), and division of the lateral iliac blade into pre- and postacetabular concavities (Figs 4, 5: fid, ci): Deinonychosauria (*Adasaurus* [Barsbold, 1983], *Deinonychus* [MCZ 4371], *Saurornitholestes* [MOR 660], and *Velociraptor* [at least one specimen; Norell & Makovicky, 1999], basal Avialae (e.g. *Unenlagia* [Novas & Puerta, 1997], *Rahonavis* and *Archaeopteryx* [Forster *et al.*, 1998]), Enantiornithes (Zhou, 1995a,b; PVL 4041-4), Ichthyornithiformes (Marsh, 1880), and Neornithes (pers. observ., many specimens).

A2. Presence of a median vertical iliac ridge (Fig. 4): *Iliosuchus* and *Megalosaurus* (Galton & Jensen, 1979), *Piatnitzkysaurus* (MACN-CH 895), *Siamotyrannus* (Buffetaut, Suteethorn & Tong, 1996), *Stokesosaurus* (Madsen, 1974), tyrannosaurids (CM 9380, USNM 8064), ornithomimids (Russell, 1972; UCMP 154579), and therizinosauroids (Barsbold, 1983).

B1. Small, unexpanded brevis shelf and fossa (Figs 4, 6): *Euparkeria* (Ewer, 1965), Ornithosuchidae (Walker, 1964; Bonaparte, 1971), Parasuchia (*Rutiodon*, UCMP 11324, 11325; *Pseudopalatus*, NMMNH 20852), Aetosauria (Walker, 1961; *Stagonolepis*, UCMP 32422), Poposauridae (Chatterjee, 1985; TMM 31025-12), Crocodylia (*Alligator*, UCMP 71672, 119043, 119045; *Crocodylus*, UCMP 123090), and *Lagosuchus* (= *Marasuchus*; Sereno & Arcucci, 1994; PVL 3870); also see Long & Murry, 1995 for various other archosaurian taxa.

B2. Large, expanded brevis shelf and fossa (Figs 4, 6: bf): Suchia (*Gracilisuchus* and *Saurosuchus* [Gauthier, 1986; Novas, 1996] as well as some Proterochampsidae and Ornithosuchidae [many PVL specimens], and *Triassolestes* [PVL 3889]), Dinosauria (Romer, 1927a; Thulborn, 1972; Galton, 1973; Santa Luca, 1980; Peng, 1992; *Coelophys* [UCMP 129618], *Dilophosaurus* [UCMP 37302], *Allosaurus* [Madsen, 1993], Alvarezsauridae and other coelurosaurs [Chiappe *et al.*, 1996]). A few birds (*Cathayornis* [Zhou, 1995b], *Patagopteryx* [Chiappe, 1996], lithornithids and Tinami [Houde, 1988; many MVZ Tinami]) have a similar structure that I consider to be non-homologous.

B3. Reduced brevis shelf and fossa (Figs 4, 6: bf): Dromaeosauridae (Ostrom, 1976b), *Unenlagia* (Novas & Puerta, 1997), and *Rahonavis* (Forster *et al.*, 1998).

C1. Preacetabular ('cuppedicus') fossa (Figs 4, 6: cf) reduced onto the pubic peduncle, but still distinct:

Deinonychosauria and *Archaeopteryx* (Norell & Makovicky, 1997, 1999; *Deinonychus*, MCZ 4371; *Saurornitholestes*, MOR 660), basal Avialae such as *Unenlagia* (Novas & Puerta, 1997) and *Rahonavis* (Forster *et al.*, 1998), and Enantiornithes (Chiappe, 1996).

C2. Preacetabular fossa reduced to the scalloped ventral edge of the iliac blade and pubic peduncle (Figs 4–6: cf):

*Patagopteryx* (MACN-N 03, 11) and Ornithurae (Marsh, 1880), including Neornithes (MVZ and UCMP specimens of Tinamidae, Ratitae, Anatidae, Galliformes, Columbiformes, Sphenisciformes, and Gaviiformes).

evolved, although the processus supratrochantericus likely indicates the origin of the small M. iliofemoralis externus (Table 2; Romer, 1923a) as a subdivision of the IF.

#### *Brevis fossa*

Other noteworthy features of the archosaurian ilium include two ventrolateral fossae (not equivalent to the concavities mentioned above): a postacetabular 'brevis' fossa in Dinosauria (Romer, 1927a; Gauthier, 1986; Novas, 1996) and a preacetabular fossa in Avetheropoda ('cuppedicus' fossa; Rowe & Gauthier, 1990; Holtz, 2000). These fossae evolved by the ventromedial expansion of a ridge or shelf that extends from the base of the central ilium near the acetabulum to the caudal (Fig. 6: mr2) or cranial (Fig. 6: mr1) ends of the medial iliac blade.

The brevis fossa (Figs 4, 6: bf) is often cited as an indicator of muscle origin shifts during archosaur evolution (e.g. Romer, 1927a; Gauthier, 1986). However, the evolutionary origin of the brevis fossa deserves consideration. This is an issue of bone surface

homology. Welles (1984: 132–133; also see Novas, 1996) assumed that the medial side of the ilium where the sacral ribs contact the ilium is equivalent to the ancestral postacetabular iliac blade, and the lateral side of the brevis fossa (the 'spine') is a neomorph. Yet the medial shelf that forms the medial side of the brevis fossa and attaches to the second sacral rib is present but unexpanded in outgroups to Dinosauria (Fig. 6; Table 3B). This medial shelf continues caudally past the sacral rib attachment toward the caudodorsal edge of the postacetabular ilium in archosaurs, including basal dinosaurs.

Thus, the medial shelf expanded ventromedially (and to a degree, the iliac blade expanded ventrolaterally) to enclose a brevis fossa in dinosaurs as well as a few Suchia (Table 3B). The lateral side of the fossa is in the sagittal plane like the rest of the iliac blade, whereas the medial shelf is medially offset from the iliac blade. Consequently, if the lateral shelf were a neomorph, the postacetabular ilium would have been offset medially during origination of the shelf. However, a medially offset postacetabular ilium is not evident in known basal dinosaur fossils. Her-

rerosauridae appears to have lost an expanded brevis fossa (Novas, 1994: 404, fig. 5, 1996), which is autapomorphic and thus not relevant for determining the ancestral dinosaurian brevis fossa morphology. Also, when the brevis fossa was reduced in Eumaniraptora (Table 3B), the lateral blade was not affected. The medial shelf was reduced concomitant with changes in tail osteology and musculature (Gatesy, 1990) and the widening of the postacetabular pelvis.

Thus the evolution of the brevis shelf is better described as the widening and deepening of a pre-existing structure (the medial shelf and also the iliac blade) rather than as a neomorph (the lateral shelf). My perspective is congruent with many others' views (e.g. Charig & Milner, 1997). This hypothesis is more parsimonious than Welles' (1984) because it does not require the absence of the medial shelf for sacral rib attachment, the medial inflection of the postacetabular ilium, and the appearance and later loss of the lateral shelf. The fossa is hence a 'novelty' only in the sense of its considerable expansion; the shelf itself is a plesiomorphy.

The evolution of the brevis fossa is congruent with proposed patterns of muscle shifts in archosaurs (Romer, 1923c; Gauthier, 1986; Novas, 1996). *M. caudofemoralis brevis* (CFB) of crocodylians originates ventral and lateral to the medial iliac shelf, from the ventrolateral postacetabular ilium, posterior sacral rib, and two proximal caudal vertebrae (Romer, 1923b). Because this region of the iliac blade is similar in fossil archosaurs, and because other Reptilia have a similar origin of the CFB, this general condition can be inferred as ancestral for Archosauria. The avian homologue of the CFB, *M. caudofemoralis pars pelvica*, originates from the ventrolateral surface of the concavitas infracristalis ilii ancestrally in Neornithes (Gadow, 1891). The brevis fossa is likely a transitional feature, indicating a shift of the CFB origin from the medial ilium, sacrum, and tail onto the ventrolateral ilium, and perhaps attachment of the ilio-ischiadic membrane to the ventral rim of the ilium (see Pelvic Membranes, pp. 154–156).

However, the extent of the fossa does not necessarily circumscribe the extent of the CFB muscle origin, as some authors have implied (Romer, 1923c, 1927a; Russell, 1972; Tarsitano, 1983). One reason is that the crocodylian CFB origin already extends partly onto the ventrolateral ilium, and thus is not confined to the medial shelf. Nonetheless, the narrowing of the fossa in Tetanurae (Rowe & Gauthier, 1990; Holtz, 2000) and eventual loss of the brevis fossa within Maniraptora (Holtz, 1994; Novas, 1997), especially Pygostylia (Chiappe, 1996), allow the inference that the brevis fossa allowed the CFB origin to shift more laterally during theropod evolution.

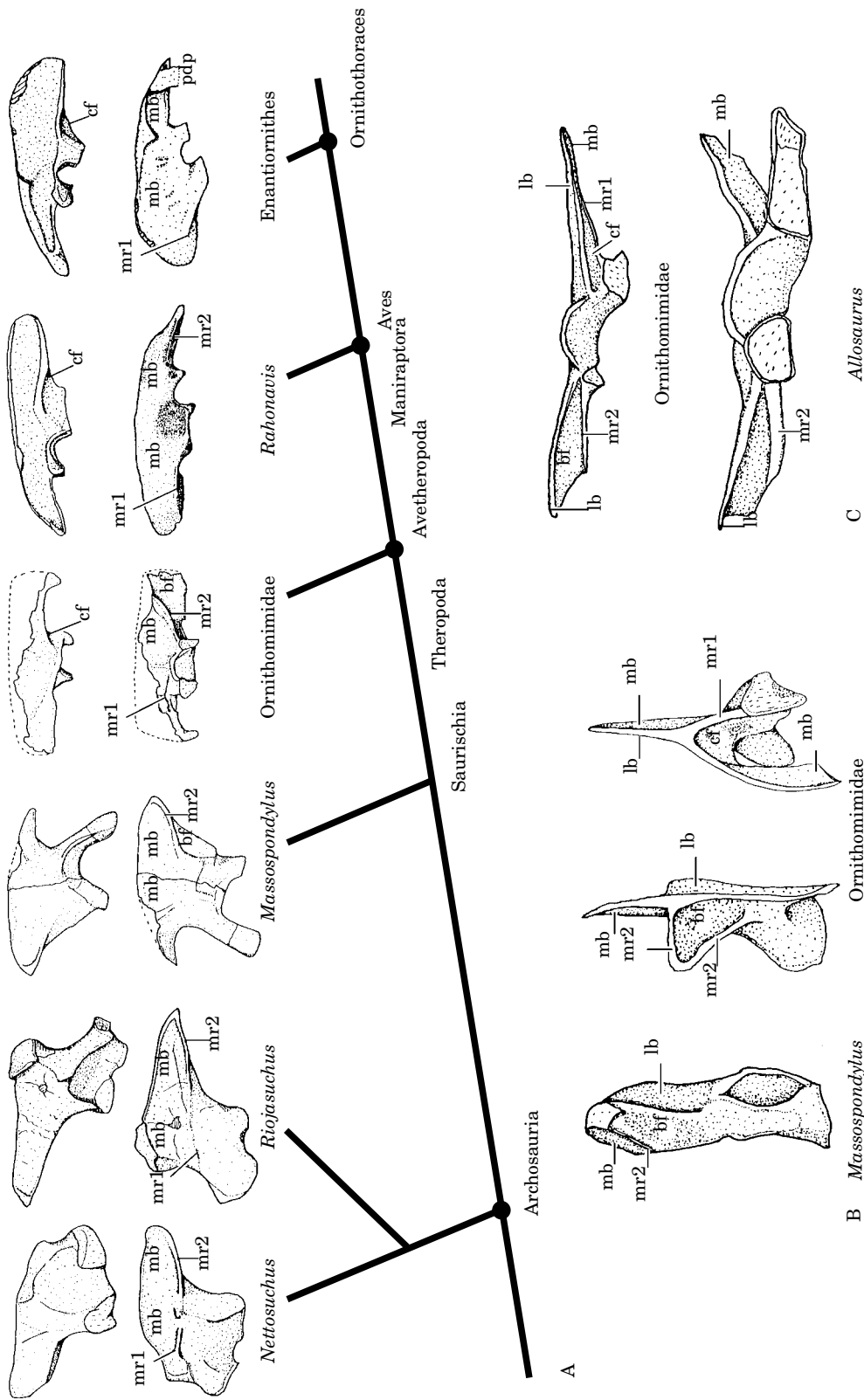
The apparent homoplastic reappearance of a 'brevis fossa' in some basal Aves (Table 3B) may seem at odds with the former inference. Yet structures similar to the brevis fossa are also present in some Neornithes (Table 3B), associated with the ilio-ischiadic membrane (see Pelvic Membranes below) rather than with *M. caudofemoralis pars pelvica* (=CFB). These avian fossae appeared after the brevis fossa was lost (failing the test of congruence) and lack similar soft tissue associations (failing the test of similarity). They are probably different characters instead of reversals to ancestral character states.

#### *Praecetabular fossa*

The preacetabular ('cuppedicus') fossa (Figs 4, 6: cf) of avetheropodan dinosaurs is also commonly thought to be evidence of the lateral shift of a muscle origin, namely *M. pubo-ischio-femoralis internus 1* (PIFI1) or its avian homologue *M. iliofemoralis internus* (IFI; Vanden Berge & Zweers, 1993; 'M. cuppedicus' of Rowe, 1986; also see Gauthier, 1986). The medial shelf of the preacetabular fossa is small, but it is plesiomorphically present in archosaurs. It expanded ventrolaterally in Avetheropoda in a pattern similar to that described above for the brevis shelf (Holtz, 2000; Sereno, 1999; Fig. 6).

The medial preacetabular shelf forms the dorsal border of the crocodylian PIFI1 origin (Romer, 1923b) and the attachment point of the first sacral rib (or sacral ribs 2 and 3 of Neotheropoda; Madsen, 1993; Novas, 1996). The crocodylian PIFI1 originates partially from the medial iliac blade, ventral sacral ribs, and medial proximal ischium (Romer, 1923a). However, the PIFI1 (=IFI of Aves) is not the only muscle located medial to the ilium in crocodylians and on its lateral surface in neornithines (Romer, 1923a,b). The PIFI2 of Crocodylia (=Mm. ilioprochanterici medialis et cranialis of Aves; Rowe, 1986) also originates from the lumbar vertebrae, cranial to the PIFI1. The many similarities in pelvic structure in basal archosaurs suggest that crocodylians retain the ancestral archosaurian condition for the PIFI (Rowe, 1986; *contra* Charig, 1972; Walker, 1977; Tarsitano, 1983; Parrish, 1986).

Hence it is possible that the preacetabular fossa is not only indicative of a lateral shift of the origin of the PIFI1, but the origin of the PIFI2 as well, or only the PIFI2. Again, the preacetabular fossa does not necessarily delimit the size or precise origin of the muscle(s) that attached to it. It is difficult to discern the borders of the PIFI1 or 2 on the preacetabular fossa, because the surfaces of the fossa are smooth without discrete muscle scars. In fact, the origins of the PIFI homologues in Neornithes are all along the ventrolateral surface of the ala preacetabularis ilii,



**Figure 6.** Evolution of iliac fossae on the line to Neornithes. A, ilia in lateral (top) and medial (bottom) view of *Nettosuchus* (Crocodylia; UCMP 38012), *Riojasuchus* (Ornithosuchidae; left ilium of PVL 3828, reversed), *Massospondylus* (Sauropodomorpha; left ilium of PVSJ 569, reversed), Ornithomimidae (UCMP 154759), *Rahnavis* (left ilium of UA 8656, reversed), and Enantiornithes (PVL 4032-3). B, ilium of *Massospondylus* (Sauropodomorpha; left ilium of PVSJ 569, reversed) in caudal view, and ilium of Ornithomimidae (UCMP 154759) in caudal (on left) and cranial (on right) view. C, ilia of *Ornithomimus* (ROM 851) and *Allosaurus* (left ilium of MOR 693, reversed) in ventral view. 'lb' and 'mb' are the medial and lateral surfaces of the ilium. 'mr1' and 'mr2' are the first and second medial ischial ridges. 'pdp' in Enantiornithes is the proximal dorsal process of the ischium, shown contacting the medial surface of the crista dorsolateralis ilii. Ilii in A and C are scaled to the same length; in B they are scaled to the same height.

so both *M. iliofemoralis internus* (=PIFI1) and *Mm. iliotrochanterici cranialis et medialis* (=PIFI2) could have originated from the preacetabular fossa. Yet available data do not clarify which muscle(s) moved laterally as the preacetabular fossa was reduced (for more discussion see Carrano, 2000).

Despite these complications, fossils reveal a possible transitional sequence from the ancestral reptilian condition of a medial PIFI to the lateral *M. iliofemoralis internus* and *Mm. iliotrochanterici medialis et cranialis* in neornithines (Figs 2, 4, 6). As the ilium expanded cranially within Theropoda, it extended over the posteriormost dorsal ('lumbar') vertebrae and eventually may have 'captured' one or more of the PIFI origins. The preacetabular fossa of Avetheropoda provides one feasible pathway for the 'capture' and lateral movement of the PIFI origins. The preacetabular fossa (i.e. the medial iliac shelf) was reduced as the lateral iliac blade extended laterally onto the pubic peduncle of the ilium in Eumaniraptora (Table 3C). The fossa was reduced as the synsacrum expanded cranially by adding more vertebrae, concurrent with a cranial expansion of the ilium.

The preacetabular shelf is absent in Alvarezsauridae (Novas, 1997) and *Patagopteryx* + Ornithurae (Chiappe, 1996), which may have had a fully lateral PIFI group. Hence the inference that the PIFI group shifted laterally on the line to Neornithes is supported by palaeontological data. Furthermore, the scalloped edge of the ilium in *Patagopteryx* (MACN-N 03, 11) as well as in many Ornithurae (Figs 5, 6: cf; Table 3C) looks much like a reduced preacetabular fossa. Whether or not this

proposed character state homology is acceptable is ultimately a subjective matter (i.e. the test of similarity), but my hypothesis is phylogenetically congruent and matches the scenario of muscle evolution outlined above (also see Rowe, 1986). At least one part of the PIFI seems to have shifted laterally within Aves, but which part(s) shifted (and when they shifted) remains unclear.

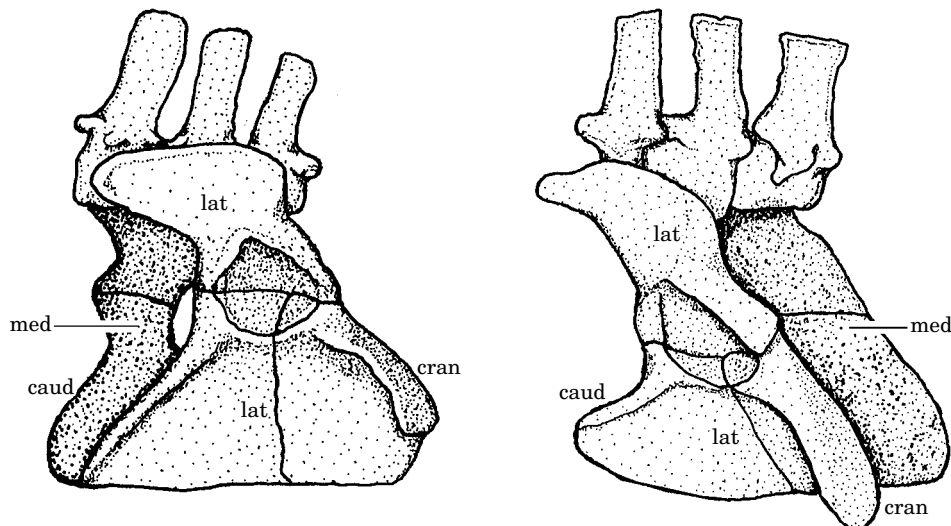
#### *Summary of iliac evolution*

A protracted pattern of expanding the ilium cranially as vertebrae were added to the sacrum predominated within Dinosauria on the line to Neornithes. A postacetabular brevis fossa enlarged in Dinosauria as the CFB moved laterally. In Avetheropoda, a preacetabular 'cuppedicus' fossa seems to reflect a shift of at least part of the PIFI from a ventromedial position to lie more laterally. *Mm. dorsales caudae et trunci* probably became more decoupled from each other within Coelurosauria. The preacetabular ilium and sacrum remained fairly narrow in most coelurosaurs as the postacetabular ilium widened, especially within Aves. The lateral iliac surface became partitioned into pre- and postacetabular concavities in Eumaniraptora, whereas the preacetabular fossa shifted more laterally. Both ventral iliac fossae reduced within Aves as their associated muscles moved fully onto the lateral iliac blade.

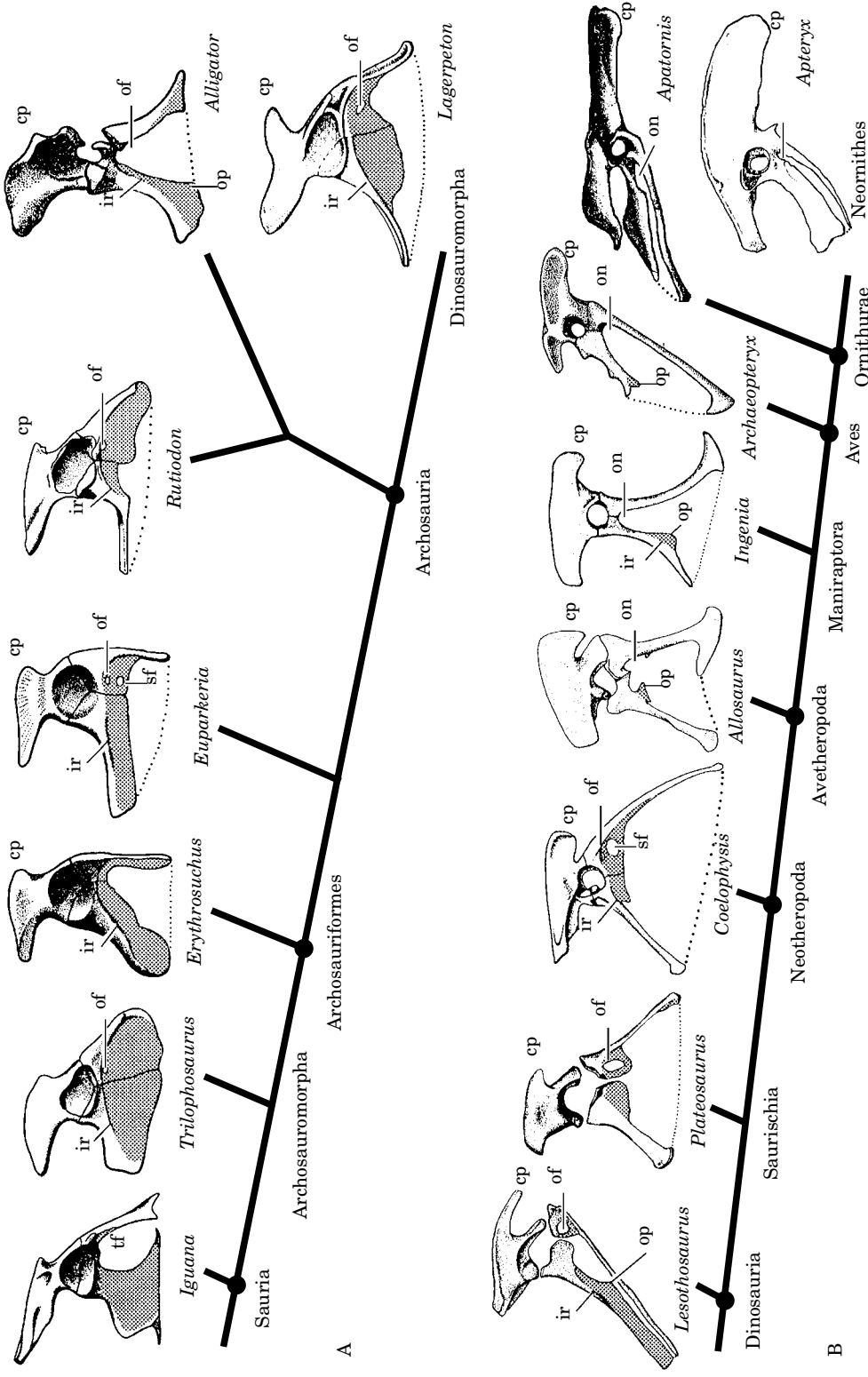
#### PUBO-ISCHIADIC PLATE

##### *Pubo-ischiadic plate surfaces*

The pubes and ischia of both extant clades of Archosauria have some salient autapomorphies, as do



**Figure 7.** Pelvic bone surfaces of the basal archosauromorph *Trilophosaurus* (left side of AMNH 7502, reversed) in caudolateral (on left) and craniolateral (on right) view. Cranial (cran), caudal (caud), lateral (lat), and medial (med) surfaces are indicated. Not to scale.



**Figure 8.** Evolution of the pubo-ischiadic plate on the saurian line to Neornithes. The dotted line along the ventral pelvis indicates the ventral boundary of the pubo-ischiadic fenestra. Darkly shaded regions are pubo-ischiadic plate surfaces. Pelvises in lateral view: A, *Iguana*, *Trilophosaurus*, *Erythrosuchus*, *Euparkeria*, *Ruitodon*, *Alligator* (all modified from Romer, 1956), and *Lagerpeton* (modified from Sereno & Arcucci, 1993). B, *Lesothosaurus* (modified from Weishampel & Witmer, 1990), *Plateosaurus* (modified from Galton, 1990), *Coelophysis* (modified from Rowe & Gauthier, 1990), *Allosaurus* (modified from Molnar, Kurzanov & Dong, 1990), *Ingenia* (modified from Barsbold, Maryanska & Osmólska, 1990), *Archaeopteryx* (modified from Chatterjee, 1997), *Apatornis* (modified from Marsh, 1880), and *Aptyeryx* (modified from McGowan, 1979). 'sf' is the secondary pubic foramen and 'tf' is the thyroid fenestra. Scaled to the same pelvic length.



the pubes and ischia of Podosauridae, Pterosauria, ornithischian and sauropod dinosaurs, as well as other extinct taxa. Homologizing pubic bone surfaces is vital for comparing them and for inferring transformations of the soft tissues that attach(ed) to the ventral pelvis. It can be difficult to delineate unambiguous boundaries on the smooth, rounded shafts of the pubes and ischia, but an evolutionary perspective provides some clarity.

The plesiomorphic condition for Reptilia is a pubo-ischiadic plate composed of laterally concave and ventrally (medially) convex symphyseal surfaces (Figs 7, 8; Romer, 1956). The plate is occupied primarily by the origins of *M. pubo-ischio-femoralis externus* (PIFE; laterally/ventrally) and *internus* (PIFI; medially/dorsally). The ancestral pubo-ischiadic symphysis is along the ventral midline; thus the most extensive areas of pubic and ischiadic surface are lateral (=ventral) and medial (=dorsal). Cranial and caudal surfaces consist of a thin ridge between the medial and lateral surfaces. Proximodistal ridges on the lateral surface of the pubes and ischia mark the ancestral boundaries between the stout, convex pubic/ischiadic shafts (cranially/caudally) and the thin, concave pubo-ischiadic plate (below the acetabulum). These ridges indicate the presence of aponeurotic boundaries between muscle attachments (such as hypaxial muscles).

One such ridge separates the lateral pubis (attachment site of *M. ambiens* and hypaxial muscles such as *Mm. obliquus abdomini internus et externus*) from the obturator foramen and the caudal surface of the pubic apron (site of the PIFE2 origin in Crocodylia and likely in many other archosaurs; see pp. 145–146). A second, ischial ridge forms the cranial boundary of the origin of *M. adductor femoris 2* (ADD2) in crocodylians, separating the origin of that muscle from the adjacent PIFE3 (Romer, 1923b). This ischial ridge is present in fossil archosauriforms, corroborating the presence of two ADD muscle heads ancestrally in Archosauria (see Ischial Structures, pp. 152–153, for more discussion).

#### *Pelvic symphyses and aprons*

Plesiomorphically, archosauriform pubes and ischia each have a medial symphysis that faces cranially and caudally (Romer, 1956). These symphyses expanded into ‘aprons’ in many archosauriforms (Figs 9, 10: pa, ia), although the aprons are small in basal taxa such as Proterosuchidae (Cruickshank, 1972). I use the term ‘apron’ to refer to the proximodistally expanded surface of the ancestral symphysis, and I use ‘symphysis’ to refer to contralateral pelvic elements that are co-ossified in adults. Therefore, an apron is a derived character state of the character ‘symphysis’—not a novel structure, but an expansion of ancestral bone surface. Pelvic elements may contact each other without forming a true symphysis, as in some Maniraptora (Norell

& Makovicky, 1997, 1999; Forster *et al.*, 1998). An apron could persist as a bone surface after its symphysis was eliminated, but the apron would still be a derivation of the ancestral symphyseal surface. This is the case for crocodylian pubes and ischia: they are not tightly coossified in a symphysis, but their apron surfaces remain.

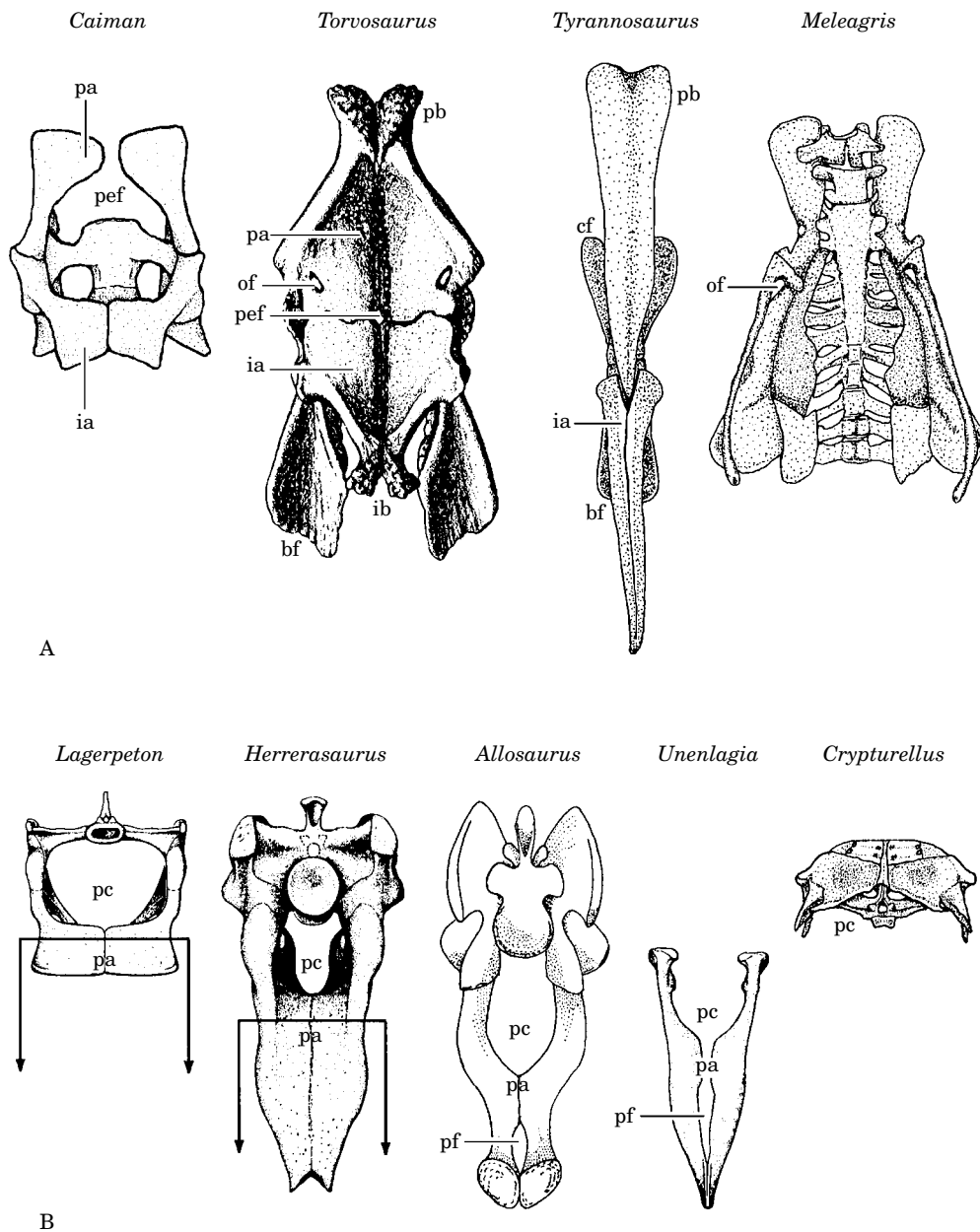
What such expanded symphyses topologically correspond to in basal archosauriforms is a question of bone surface homology. As the symphyses elongated to form aprons, their cranial and caudal surfaces would have been greatly expanded. Although crocodylian pubes are mobile, secondarily shortened, lack an ossified symphysis, and are excluded from the acetabulum (Benton & Clark, 1988; Russell & Wu, 1997), they do not show any signs of rotation or other shifting of their surfaces from their ancestral positions. I contend that crocodylian pubic osteology and myology is not as autapomorphic as some authors have presumed (Romer, 1923b; Walker, 1977; see below), although some autapomorphies are present.

The extensive cranial (=‘dorsal’) or caudal (=‘ventral’) surfaces of crocodylian (and other archosaur) pubes are equivalent to the cranial or caudal pubic apron surfaces of more basal archosauriforms (and the lateral or medial surfaces of the ancestral pubo-ischiadic plate). The lateral and medial pubic surfaces consist mostly of the thin pubic shaft. In contrast, the most extensive ischial surfaces remain lateral and medial in crocodylians and other archosaurs. Thus the cranial and caudal pubic surfaces expanded as the pubes elongated, unlike the ischia. In archosaurs with distal symphyses that are cranially and/or caudally expanded into ‘boots’ (e.g. Podosauridae, Herrerasauridae, and Tetanurae), mainly the lateral surface is expanded (see Pubic Structures, pp. 146–148).

#### *Pubo-ischiadic plate reduction*

The pubo-ischiadic plate opened up independently in all four extant clades of Reptilia (Fig. 8), producing separate pubic and ischiadic regions. This change is correlated with subdivided PIFE and PIFI musculature (Romer, 1922, 1923a,b,c, 1956; Walker, 1977). The pubo-ischiadic plate was absent once birds lost the pubic apron and ischial obturator process (see, p. 141). The fragmentation of the pubo-ischiadic plate resulted from three interrelated changes:

(1) Chelonians and lepidosaurs evolved a ‘thyroid fenestra’ (Romer, 1956; Fig. 8: tf) within the concave region of the pubo-ischiadic plate, but ancestrally maintained a ventral symphysis. In contrast, archosauriforms elongated the pubes and ischia to form an open pubo-ischiadic fenestra between them (Fig. 8). Such fenestration is most prominent in Suchia and Dinosauriformes, and apparently was secondarily

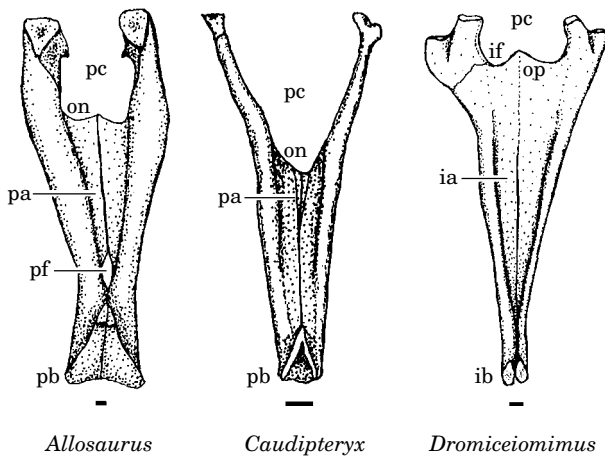


**Figure 9.** A, ventral view of archosaur pelves: *Caiman* (Crocodylia; UCMP 132077), *Torvosaurus* (basal Tetanurae; modified from Galton & Jensen, 1979), *Tyrannosaurus* (Tyrannosauridae; MOR 555), and *Meleagris* (Neognathae; UCMP 156152). 'pef' is the pelvic fenestra. Not to scale. B, dinosauromorph pubic apron features. The bracket and arrows indicate how the distal pubic symphysis elongated cranioventrally within Dinosauromorpha to form the pubic apron. Pelves figured in cranial view: *Lagerpeton* (Dinosauromorpha; modified from Sereno & Arcucci, 1993), *Herrerasaurus* (Herrerasauridae; modified from Novas, 1993), *Allosaurus* (Carnosauria; modified from Molnar *et al.*, 1990), *Unenlagia* (Eumaniraptora; modified from Novas & Puerta, 1997; ilium and sacrum omitted), and *Crypturellus* (Paleognathae; MVZ 85503). Note that the pubis is retroverted so far in *Crypturellus* that it is barely visible, and the pubic apron is absent. Scaled to the same pelvic width.

reduced in *Doswellia*, Proterochampsidae, and Pterosauromorpha (Padian, 1983; Benton & Clark, 1988).

Unlike thyroid fenestrae, the pubo-ischiadic fenestra

may not have been occupied by limb musculature (Romer, 1956). As discussed below, the pubo-ischiadic fenestra of archosauriforms is bounded cranially and



**Figure 10.** Pelvic aprons in theropod dinosaurs. Pubes of *Allosaurus* (Carnosauria; MOR 693) and *Caudipteryx* (Oviraptorosauria; NGMC-97-4A) in caudal view, and ischia of *Dromiceiomimus* (Ornithomimosauria; AMNH 5201) in cranial view. Scale bar = 1 cm.

caudally by the elongated pubic and ischiadic symphyses, not by the portions of the pubes and ischia that are proximal to the symphyses. The pubo-ischiadic fenestra is not within the pubo-ischiadic plate (unlike a thyroid fenestra), but rather is ventral to and surrounded by the boundaries of the ancestral pubo-ischiadic plate. Therefore, this fenestration was more like 'pseudofenestration'—it did not involve the elimination of bone surfaces, but rather was the localized elongation of bone surfaces to enclose space outside the ancestral pubo-ischiadic plate (Romer, 1956).

As Romer (1956: 324; also see Walker, 1977) intimated, the archosauriform pubic apron corresponds to the transverse ancestral reptilian symphysis that elongated cranioventrally beneath the pelvic canal. This elongation left the proximal portion behind, especially the anterior part of the pubo-ischiadic plate. Likewise, the ischiadic symphysis elongated caudoventrally to form the ischiadic apron, leaving the proximal (cranial) symphysis behind (Figs 8–10; see #2 below). Evidence for this localized extension includes the proximal structures such as the obturator foramen, obturator process and notch, pubic tubercle, and ischial tuberosity, discussed below. These structures did not move distally with elongation of the pubes or ischia, whereas some hypaxial musculature (e.g. Mm. rectus abdomini internus et externus) did move distally with the symphyses. The distalmost pubes and ischia (i.e. ventral to the pelvic canal) elongated, not the entire ventral pelvis isometrically—otherwise the aprons would not have formed and the symphyses would only be distal.

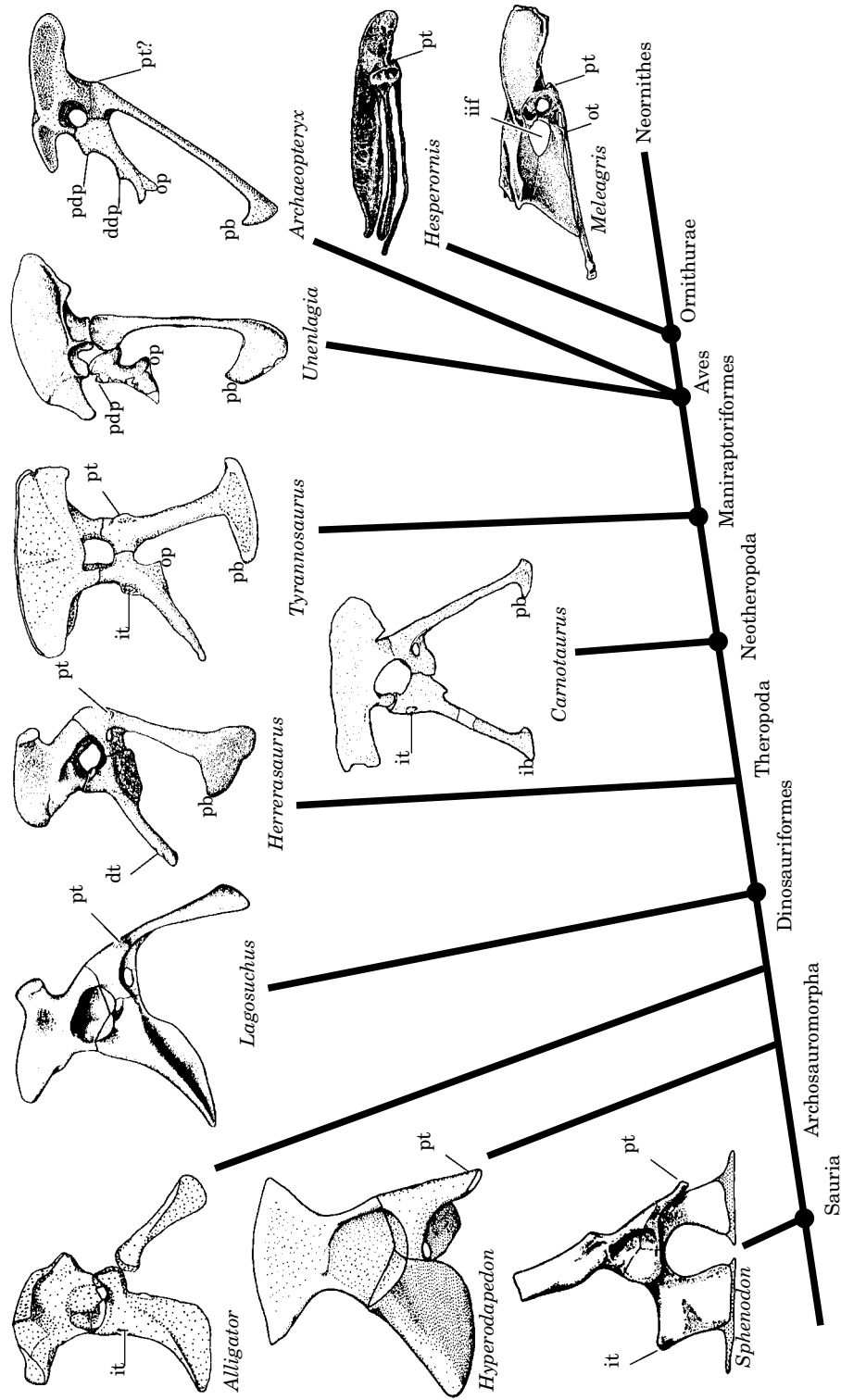
(2) Reducing the pubic and ischiadic aprons is a

second mode of reducing the ancestral pubo-ischiadic plate. It involves the elimination of the transverse bone surfaces. The ventral surface of the pelvic canal was ancestrally complete (or nearly so) between the ischiadic and pubic symphyses in Reptilia. It remained continuous in Archosauriformes (Figs 9, 10: pc). This ventral floor of the pelvic canal was eliminated many times within Archosauriformes, opening a ventral pelvic fenestra (Fig. 9A: pef). The pelvic fenestra is more or less open in Proterochampsidae (Romer, 1972) and apparently in *Lagosuchus* (Serenio & Arcucci, 1994), as well as within Suchia (Walker, 1961, 1964; Chatterjee, 1985), Pterosauriformes (Padian, 1983), Ornithischia (Thulborn, 1972; Santa Luca, 1980; Sereno, 1991b), Sauropodomorpha (Huene, 1926; Bonaparte, 1971), and Tetanurae (Currie & Zhao, 1994; Charig & Milner, 1997). Character optimization is problematic because of missing data: this feature is seldom well preserved or described.

The reduction of symphyseal bone surfaces forms a ventral pelvic fenestra within the ancestral pubo-ischiadic plate, unlike the pubo-ischiadic fenestra. In theropods, the reduction of the pubic apron began within Neotheropoda (especially Avetheropoda) and continued in Maniraptoriformes as the pelvic canal widened (Norell & Makovicky, 1997). The apron was eliminated in some Alvarezsauridae as well as *Patagopteryx* + Ornithurae (Chiappe, 1996; Novas, 1997). The reduction of the pubic apron proceeded mostly from proximal to distal, although some fenestration (the pubic foramen; Figs 9, 10: pf) appeared in the distal pubic apron of Neotheropoda. Pubic apron reduction is correlated with the retroversion of the pubes (except in *Herrerasaurus*) and the loss of pubic symphysis or contact. Its result on the line to Neornithes is that avian pubes mainly have flat medial and lateral surfaces separated by thin cranial and caudal ridges. Most of the ancestral cranial and caudal pubic surfaces were eliminated along the line to Neornithes.

The ischial apron, including the obturator process, was reduced in a pattern similar to the pubic apron (see Ischial Structures, pp. 152–153). It became narrower within Saurischia and was reduced as the obturator process moved distally within Tetanurae. The ischial symphysis split in Aves but was already reduced in most Maniraptora. This reduction was concurrent with pubic retroversion, the widening of the postacetabular pelvis (see Iliac Structures, pp. 132–133), and modifications of the tail (Gatesy, 1995).

Besides reducing the pubo-ischiadic plate, the opening of pelvic fenestrae eliminates surfaces that would have ancestrally served as muscle origins, especially for the PIFI and PIFE. If the PIFI originated only from the ventral floor of the pelvic canal in basal archosaurs (although this seemingly is not the case;



**Figure 11.** Evolution of the pelvis and ischium on the saurian line to Neornithes. Pelvis in lateral view: *Sphenodon* (modified from Romer, 1956), *Hyperodapedon* (modified from Benton, 1983), *Alligator* (UCMP 138037), *Lagosuchus* (modified from Sereno & Arcucci, 1994), *Herrerasaurus* (modified from Novas, 1994), *Carnotaurus* (modified from Bonaparte *et al.*, 1990), *Tyrannosaurus* (MOR 555), *Unenlagia* (modified from Novas & Puerta, 1997), *Archaeopteryx* (modified from Chatterjee, 1997; all scaled to the same pelvic height), *Hesperornis* (modified from Marsh, 1880), and *Meleagris* (modified from Baumel & Witmer, 1993; both scaled to the same pelvic height). 'ddp' is the distal dorsal process of the ischium.

Rowe, 1986), the evolution of PIFI might have proceeded differently on the lines to Crocodylia and Neornithes. In that scenario, crocodylians might not retain the ancestral archosaurian PIFI condition. However, character optimization suggests that crocodylians do have the two heads of the PIFI that are ancestral for Reptilia (Rowe, 1986). Furthermore, crocodylians retain a partly ventral PIFI1 origin, from the medial ischium (Romer, 1923a) and hence retain an intermediate character state in the dorsal migration of the PIFI.

(3) Opening foramina in the pubo-ischiadic plate also reduces it, and this can happen in several ways. Secondary 'thyroid' foramina perforate the proximal pubes distal to the obturator foramen (i.e. the lateral side of the ancestral pubo-ischiadic plate) in *Euparkeria*, *Riojasuchus*, *Stagonolepis*, and some coelophysoid theropods (Fig. 8: sf; Benton & Clark, 1988; Rowe & Gauthier, 1990), reducing the pubo-ischiadic plate proximal to the pubic apron. The pubic foramen (Figs 9, 10: pf) reduced the pubic apron surface. The significance of such foramina is unclear. They may have served as passages for one or more branches of *N. obturatorius* and/or other soft tissues. Unfortunately, extant taxa are of little help in interpreting the anatomical significance of such foramina because these structures are unique to extinct taxa. However, Martill *et al.* (2000) propose a feasible hypothesis that the pubic foramen may have accommodated a ventral pneumatic duct leading to a post-pubic air sac. Other foramina such as the obturator foramen (see Pubic Structures below) and ischial foramen (see Ischial Structures, p. 152) may eliminate their ventral boundaries to reduce the pubo-ischiadic plate.

#### *Summary of pubo-ischiadic plate evolution*

A protracted pattern of elongating the pubes (cranioventrally) and ischia (caudoventrally) predominated within Archosauriformes on the line to Neornithes. Pubic and ischial aprons were formed as expansions of the distal symphysis. This expansion created a 'pseudo-fenestra' between the pubes and ischia; the ventral symphyseal surfaces remained closed. The expansion was associated with reduction of the pubo-ischiadic ligament and presumably the flexor cruris muscles. Ischial scarring indicates that the ancestrally single ADD split into its two archosaurian heads at roughly the same time. The pubo-ischiadic plate reduced from proximally to distally within Tetanurae by opening foramina into fenestrae and reducing the ossification of the symphyses. Birds lost the pubo-ischiadic plate through a series of changes. The ischial apron was lost within Aves, and the pubic apron was lost in *Patagopteryx* + Ornithurae.

## PUBIC STRUCTURES

### *Obturator foramen*

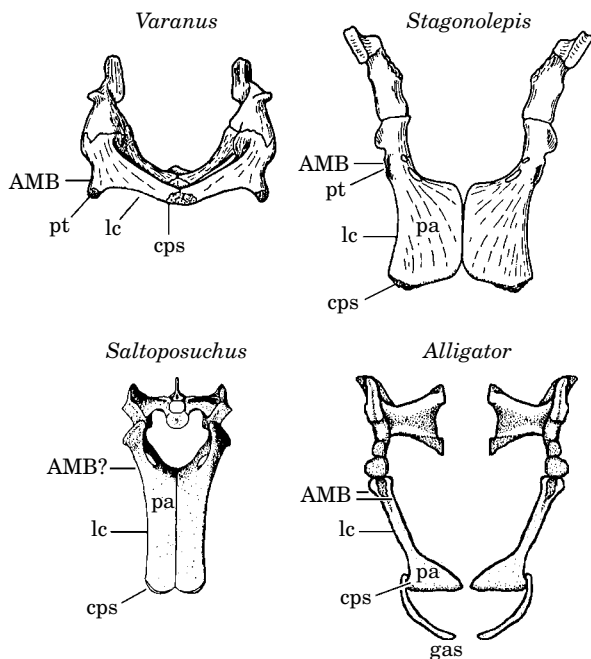
An obturator foramen (Figs 8, 9: of) for the passage of *N. obturatorius* is ancestrally present in Reptilia on the proximal pubis, cranioventral to the acetabulum. This foramen was 'lost' convergently within Chelonia, Crocodylia, Ornithischia, and Avetheropoda. Thus in these taxa the obturator nerve passed laterally through the pubo-ischiadic fenestra to the hindlimb. The obturator foramen was lost in theropods by the elimination of the ventral border of the foramen, leaving an obturator notch (Figs 8, 9: on) that opens into the pubo-ischiadic and pelvic fenestrae (Currie & Zhao, 1994; Charig & Milner, 1997; Holtz, 2000). The neornithine obturator foramen lies between the proximal pubis and ischium in the pubo-ischiadic fenestra, not within the pubis, and hence is a different character state from the ancestral reptilian condition. Fossils reveal that this characteristic evolved earlier within Tetanurae.

### *Pubic tubercle*

The pubic tubercle (Figs 11–13: pt; =processus lateralis pubis, pubic tuberosity, preacetabular tubercle, or pectineal process) was ancestrally present in Reptilia (Romer, 1956) and appears early in reptilian development (Romer, 1927b, 1942). It varies in prominence among reptiles, but generally serves as the attachment for pelvic ligaments, *M. obliquus abdominus*, and sometimes *M. ambiens* (AMB). For example, lepidosaurs, chelonians, and other non-archosauriform reptiles ancestrally have a large pubic tubercle. It extends ventrolaterally and cranially from the cranio-lateral base of the proximal pubis, proximal to the obturator foramen.

This large tubercle is present in basal Archosauriformes, but is only represented by a proximal cranio-lateral rugosity in Archosauriformes (Table 4). It is absent or strongly reduced in Crocodylia (Romer, 1923b; pers. observ.). The reduction of the pubic tubercle in archosauriforms is correlated with the loss of *M. pubotibialis* (Romer, 1923b,c; Fig. 2: PUT) and the reduction of the pelvic ligaments (see pp. 145, 156–158). Soft tissue correlation with the pubic ('ambiens') tubercle is probably not as simple as most authors have presumed. The AMB probably attached there (or nearby) in many taxa, but the pelvic ligaments and *M. obliquus abdominus* are also associated with the pubic tubercle.

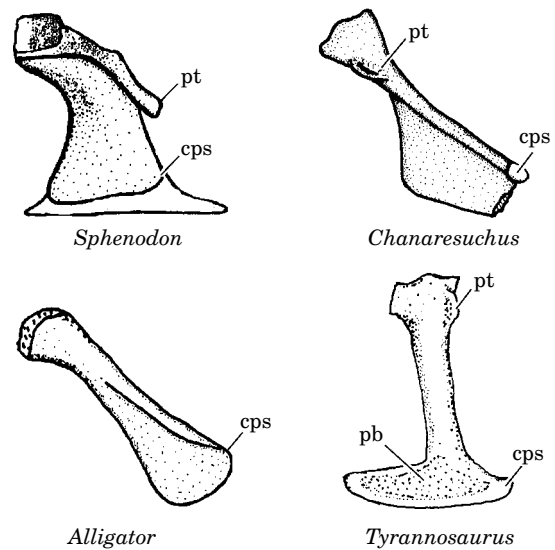
Some basal archosauriforms (e.g. *Tropidosuchus*, PVL 4601 and *Lagerpeton*, PVL 4679) appear to have two tuberosities on the pubis: one proximal, corresponding to the pubic tubercle of this study (Figs 12, 13: pt), and one distal, corresponding to the 'processus



**Figure 12.** Pubic bone surface homologies. Pelves in cranial view: *Varanus* (Lepidosauria; modified from Walker, 1977), *Stagonolepis* (Aetosauria; modified from Walker, 1977), *Saltoposuchus* (basal Crocodylomorpha; modified from Crush, 1984), and *Alligator* (Crocodylia; UCMP 131699); also see Fig. 9B for Dinosauromorpha. 'lc' is the concave lateral edge of the pubis and 'gas' is the posteriormost gastralium. Scaled to the same pelvic width.

lateralis pubis' of Walker (1977; Figs 12, 13: cps) or the pubic boot (Fig. 13: pb; Parrish, 1991). These two tuberosities may have diverged from a single ancestral location. They could have split from the same ancestral structure or one could be a 'neomorph'; unfortunately, evidence is inconclusive. The distal tubercle (including the pubic boot) may have been associated with *M. rectus abdominus* attachment and fibrous connections between the distal pubes and ischia (as suggested by Parrish, 1991). This soft tissue anatomy is present in most extant Reptilia, including Crocodylia and Neornithes (Gadow, 1882b, 1891).

The ornithischian 'prepubis' presumably is a cranially elongated pubic tubercle for pelvic ligament, hypaxial muscle and AMB attachments (Romer, 1927a; Galton, 1969; Charig, 1972; Walker, 1977; Santa Luca, 1980). This homology is tenable because the base of the prepubis is proximal and cranial to the obturator foramen and close to the acetabulum, like the ancestral pubic tubercle. The rugosity also elongated cranially into a crest in some Tyrannosauridae and most Eumaniraptora, especially birds (Table 4). The preacetabular tubercle of many Neognathae develops mostly from the ilium (unlike in Paleognathae and



**Figure 13.** Reptilian pubes in lateral view: *Sphenodon* (Lepidosauria; modified from Romer, 1956), *Chanaresuchus* (Proterochampsidae; PVL 4575), *Alligator* (Crocodylia; UCMP 138037), and *Tyrannosaurus* (Tyrannosauridae; MOR 555). Note the proximal rugosity (pubic tubercle) and distal rugosity (craniolateral surface of the pubic symphysis). Scaled to the same pubis length.

many other birds; Bellairs & Jenkin, 1960). Rather than consider the tubercle a new, unique character, it is simpler to presume that the development of the tubercle has evolved to a derived character state (relatively more contribution of the iliac anlage to the preacetabular tubercle). All of these traits are different character states of the pubic tubercle (not distinct characters) despite their variation in shape and prominence (Table 4).

#### *Walker's (1977) homologies*

Using the criteria of homology discussed above, Walker's (1977: 321–326, fig. 2) interpretation of the homology of the pubic tubercle (Figs 11–13: pt; his 'process lateralis pubis') is not strongly supported. This problem has repercussions for his conclusions regarding archosaur pelvic muscle homologies and evolution. His justification for homologizing the craniolateral corner of the distal pubic apron of archosauriforms, such as *Stagonolepis* (Fig. 12: cps), with the 'process lateralis pubis' (=pubic tubercle) of lepidosaurs was his inference that *M. rectus abdominus* attached there in both taxa. Walker compared the proximal rugosity (=pubic tubercle) of archosaurs (Fig. 12: pt) with the region of the AMB origin in squamates (Fig. 12: AMB). However, as discussed above, most archosauriforms have a reduced pubic tubercle that is restricted to a proximal rugosity. The craniolateral corner of the distal

**Table 4.** Taxonomic variation of the pubic tubercle (Figs 11–13: pt)**A1. Large pubic tubercle:**

Rhynchosauria (Benton, 1983), *Trilophosaurus* (TMM 31025-140), Proterosuchidae (Cruickshank, 1972), and Erythrosuchidae (Charig & Sues, 1976).

**A2. Pubic tubercle reduced to a rugosity:**

*Doswellia* (Weems, 1980), *Euparkeria* (Ewer, 1965), Proterochampsidae (Romer, 1972), and Archosauria (Walker, 1964; Sereno & Arcucci, 1993, 1994). The rugosity is well known in Ornithosuchidae (Walker, 1964) and most Crurotarsi (Bonaparte, 1971; Long & Murry, 1995), including Parasuchia (*Rutiodon*, UCMP 25791, 32160), Aetosauria (*Desmotosuchus*, UCMP 25945, 25951, 25955, 32151), Podosauridae (Chatterjee, 1987; *Poposaurus*, UCMP 25963, 25997, 25999; *Postosuchus*, UCMP 34469, 34470), and basal Crocodylomorpha (cf. *Sphenosuchus* [UCMP 129740]). It is also present in sauropodomorphs (Huene, 1926) and theropods such as *Herrerasaurus* (Novas, 1994), *Coelophysis* (CMNH 10871), *Marshosaurus* (Madsen, 1976), and Ornithomimidae (contra Russell, 1972; RTMP 94.12.603, 67.20.230).

**A3. Pubic tubercle extended cranially as a crest or spine (= preacetabular tubercle of Aves):**

Tyrannosauridae (Romer, 1923b; MOR 769; *Tyrannosaurus*, MOR 555, CM 9380; *Gorgosaurus*, AMNH 5458, ROM 1247) and Eumaniraptora (Baumel & Witmer, 1993; Hou & Zhang, 1995; Norell & Makovicky, 1997; Hutchinson & Chiappe, 1998; cf. *Troodon*, MOR 553S).

pubic apron of archosauromorphs is not parsimoniously interpreted as the homologue of the lepidosauromorph pubic tubercle. This is because the bone surface homologous with the craniolateral corner of the distal pubic apron (=the ancestral reptilian pubic symphysis) is present in basal reptiles, distal to the pubic tubercle (Figs 12, 13: cps). Consequently, Walker's (1977) proposition of homology does not seem to pass the test of conjunction.

The proximal pubic rugosity (Figs 12, 13: pt) is a better candidate for the homologue of the pubic tubercle. The pubic tubercle is at or slightly distal to the origin of the AMB (and *M. pubotibialis*, which is absent in Archosauria) in extant Reptilia, and some pelvic ligaments and muscles also attach there (see Pelvic Ligaments, pp. 156–158). In non-archosaurs, it is the attachment point of *M. rectus abdominus*. In archosaurs and some archosauriform outgroups, the gastralia (and *M. rectus abdominus*) attach to the craniolateral corner of the distal pubes (Gadow, 1882b; Romer, 1923b; Tarsitano, 1991). This requires a shift of *M. rectus abdominus* off the pubic tubercle onto the distal pubes in archosaurs including *Stagonolepis*. A

phylogenetic context using fossils reveals that the pubic tubercle remained on the proximal pubis as the distal symphysis elongated cranioventrally (see pp. 137–141). If my perspective is correct, Walker's (1977) proposition of homology passes neither the test of similarity nor the test of congruence.

There are additional inconsistencies. The PIFI of all Reptilia passes directly above the pubic tubercle toward its insertion on the craniolateral surface of the proximal femur (Fig. 14A). I consider the craniolateral edge of the distal pubes in Crocodylia (Figs 12, 13: cps) to be homologous with the same point in other archosaurs (given their topological similarity and no compelling contrary evidence). However, in Crocodylia the PIFE1 (not the PIFI1) passes directly above that area (Fig. 14A). Walker explained this inconsistency by asserting that crocodylian pubes are autapomorphic, and that the equivalent of the pubic tubercle in Crocodylia is on the proximal (not distal) pubes.

Accepting the latter hypothesis would require evidence for a complex scenario involving three major changes on the line to Crocodylia (i.e. within Crurotarsi): (1) the pubic tubercle moved proximally as (2) the PIFI1 ('pars ventralis') moved off the pubes and (3) the PIFE1 moved onto the pubes. Fossils of basal archosaurs (Figs 12, 13) falsify the first point: no pubic landmarks cited by Walker shifted their relative positions proximally on the lineage leading to Crocodylia. No evidence supports or falsifies (2) or (3) because muscle scars are not visible on the pubic apron. Yet because the surface of the pubic apron shows no striking changes after it elongated within Archosauriformes (except secondarily shortening within Crocodyliformes as the apron reduced distally), it seems simplest to infer that the PIFE1 + 2 muscles in extant Crocodylia retain the ancestral archosaurian condition, as theropods would have. Finally, both extant clades of archosaurs have dorsally shifted origins of the PIFI. Therefore, given no compelling contrary evidence, it is more speculative to contend that Crocodylia and Neornithes acquired these dorsal origins independently than to accept dorsally shifted origins as ancestral for Archosauria (Rowe, 1986). Hence little compelling evidence for Walker's hypothesis exists.

This issue is not trivial. Walker (1977) used his proposed homologies of these structures as the crux of his argument that the PIFI1 (his 'ventralis'; = PIFI1 + 2 of Lepidosauria; see Romer, 1942; Rowe, 1986) originated from the cranial surface of the pubic apron in archosaurs. This was the basis of his argument against Romer's (1923a,b,c) inference that the PIFI musculature had migrated dorsally from the ventral pelvic canal in basal archosaurs. Walker suggested that this dorsal migration happened independently in crocodylians, ornithischians, and birds in conjunction

with pubic changes (such as retroversion). He posited that theropods did not have this dorsally migrated PIFI1; hence theropods were ‘unlikely’ ancestors for birds. The available data do not support Walker’s (1977) major conclusions about PIFE and PIFI origins, pubic specializations, locomotor function in archosaurs, or theropod evolution.

This apparent contradiction exemplifies Witmer’s (1995) ‘inverted pyramid of inference’—seemingly innocuous assumptions of character (and character state) homologies can be a precarious foundation on which to base higher-level evolutionary inferences. One could say that I am making the same mistake by advocating an alternative hypothesis, but my hypothesis is well supported by more detailed anatomical information in an explicit phylogenetic context. If, as considered above (p. 142), the pubic tubercle diverged into proximal and distal portions in Archosauriformes, then both my hypothesis and Walker’s (1977; also see Parrish, 1991) would be supported, yet my conclusions about thigh muscle origins would remain unaltered. Crocodylia has all of the soft tissue features that ancestrally connect to those parts, yet still has a PIFE1, not a PIFI1, origin from the cranial surface of the pubes (Fig. 14).

My revision of pubic bone surface homologies is congruent with an origin of the PIFE1, not the PIFI1, from the cranial surface of the pubic apron (Fig. 14) in archosaurs. Romer (1923c) did not come to the same conclusion for saurischians. His reasoning was that the posteriormost gastralium (Fig. 12: gas), which is ligamentously attached to the craniolateral surface of the distal pubis, is not quite as robust in saurischians as in crocodylians. This gastralium serves as part of the crocodylian PIFE1 origin, but the PIFE1 origin is also from the epipubic cartilage and the cranial (= dorsal) pubis. In fact, the PIFE1 origin from the gastralium is small compared to its extensive origin from the pubis (Fig. 14).

Despite the autapomorphic pubes of crocodiles, the pubes of other Crurotarsi and non-ornithurine Ornithodira are similar enough to infer the origin of the PIFE1 from the cranial surface of the pubic apron (Fig. 14C). This is an equivocal inference (“level 2 inference” of Witmer, 1995, 1997)—Crocodylia has both the soft tissue feature (the PIFE1) and its osteological correlate (the expansive cranial surface of the pubic apron), whereas Neornithes lacks both features. Because the PIFE1 osteological correlate is also present in basal archosaurs, I suggest that this muscle origin is a derived feature of Archosauria (and potentially in outgroups such as *Euparkeria*). The concave lateral edge of the pubic apron (Fig. 12: lc) noted by Walker (1977) corresponds to the pulley for the PIFE1 as it rounds the edge of the pubis (Fig. 14), toward its insertion on the caudolateral surface of the proximal femur (‘greater trochanter’). It is less speculative to infer the ancestral

origin of the PIFE1 from the cranial surface of the pubic apron than to propose that this similar expansive bone surface served as an attachment for another soft tissue(s) ancestrally in Archosauria, but then lost that association in crocodylians to gain a PIFE1 head.

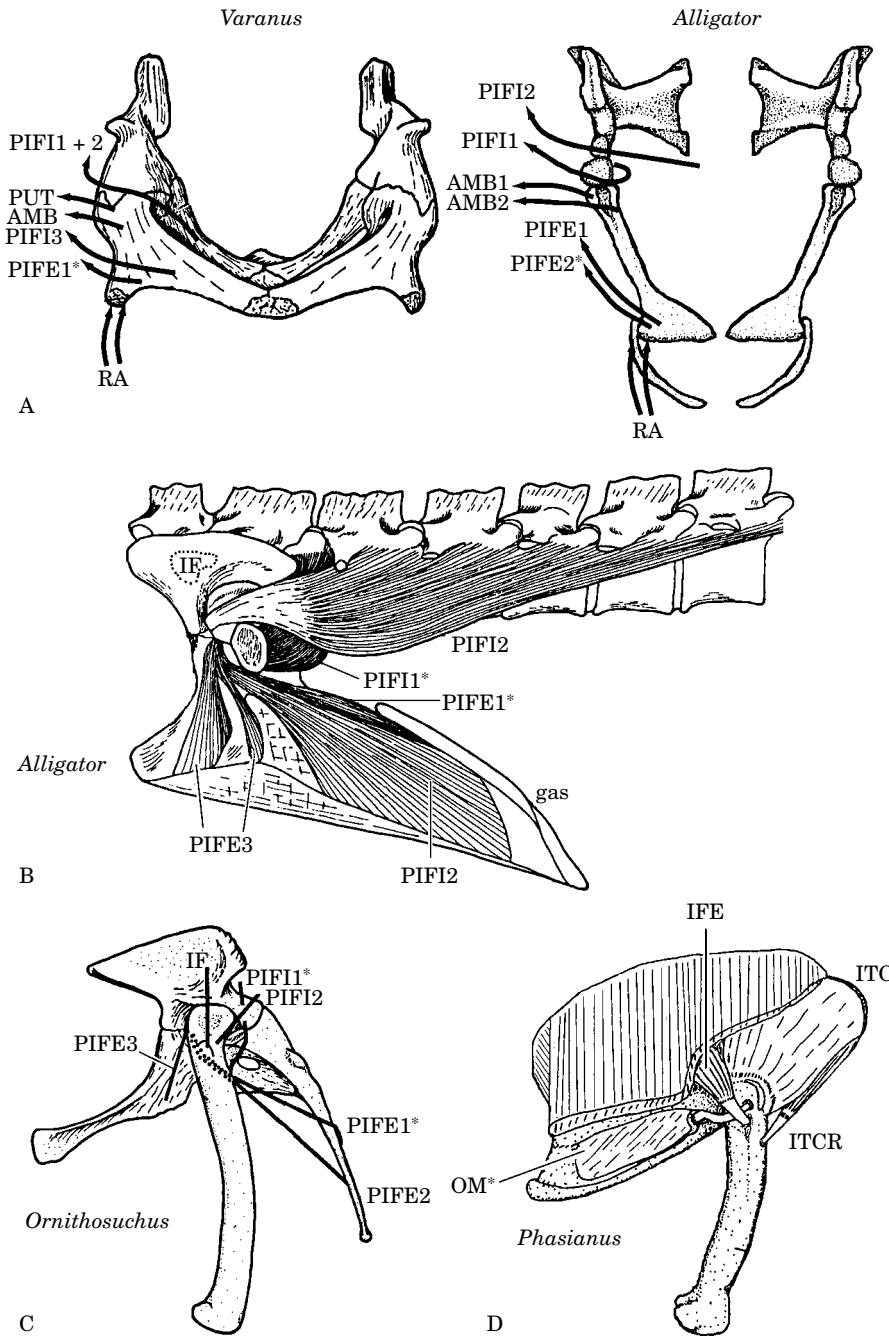
The PIFE1 probably is not a crocodylian autapomorphy as Romer (1923b,c), Charig (1972), Walker (1977), Parrish (1983), Tarsitano (1983), and others have presumed. *Ad hoc* assumptions of crocodylian autapomorphy are unjustifiable—methods and evidence, not special pleading, are used for rigorous muscle reconstruction in extinct taxa (Bryant & Russell, 1992; Witmer, 1995). Crocodylian pubes are autapomorphic in some aspects, but such specializations are not themselves evidence for additional specializations without independent anatomical evidence and support from character optimization.

As the PIFI origins shifted dorsally within Archosauromorpha from their ancestral position in this region, the PIFE1 could have taken their place (Fig. 6C), moving onto the expanded cranial surface of the pubic apron. When the pubic apron was lost in *Patagopteryx* + Ornithurae, the PIFE1 may have reduced and shifted slightly laterally to become the small pubic M. obturatorius lateralis (OL) of Neornithes. When the PIFE1 reduced to become the OL, the PIFE2 may have moved medially to become M. obturatorius medialis (Romer, 1927a,b; also see Pelvic Membranes, pp. 154–155 [OM]). The PIFE2 origin already lay inside the pubo-ischiadic fenestra (on the caudal surface of the pubic apron) and may have shifted caudomedially to become the OM of Neornithes when the apron was lost. This hypothesis is supported by ontogenetic data (Romer, 1927b; Bellairs & Jenkin, 1960). A similar change may have evolved independently in other lineages such as Ornithischia and Alvarezsauridae. Chatterjee (1997: 174) posited that the PIFI, not the PIFE2, originated from the pubic apron in Maniraptora and later became the OM. This hypothesis is not well supported by any neontological or palaeontological data.

#### *Pubic boot and retroversion*

As discussed above, some archosaurs evolved a pubic boot (Figs 11, 13: pb) that is a craniocaudal expansion of the lateral bone surface. The pubic boot is not an expansion of pubo-ischiadic plate surface, because it is distal to that surface and is an expansion of the lateral surface of the distal symphysis. It probably served mainly for abdominal muscle attachment (cranially: M. rectus abdominus and M. obliquus abdominus; caudally: M. ischiocaudalis) because lateral pubic bone surfaces, especially distally, are regions of abdominal muscle attachment in all Reptilia (Gadow, 1882b, 1891; Romer, 1922, 1923b). Connective tissues





**Figure 14.** Reptilian pelvic muscles, with an emphasis on archosaur pubic musculature. Rough lines of action of muscles are indicated. For clarity, not all thigh muscles are shown in all drawings. A, pelvises of *Varanus* (modified from Walker, 1977) and *Alligator* (UCMP 131699) in cranial view. B through D, right hindlimbs and thigh musculature in lateral view: B, *Alligator* (modified from Walker, 1977). C, *Ornithosuchus* reconstructed (modified from Walker, 1977). D, *Phasianus* (Neognathae; my dissection). See Table 1 for muscle abbreviations; 'RA' is *M. rectus abdominus*. Abbreviations ending in an asterisk (\*) originate medial to the point indicated (i.e. behind the surface shown). Not to scale.

spanning the gap between the distal pubes and ischia are also present in most Reptilia, and hence are also correlated with the pubic (and ischial) boot (Parrish, 1991).

The pubic boot originated as a knoblike structure in basal Theropoda, expanded craniocaudally into a large boot within Tetanurae, lost its cranial expansion within Maniraptora (Gauthier, 1986; Rowe & Gauthier, 1990;

Holtz, 1994), and lost its caudal expansion in *Patagopteryx* + *Ornithurae* (Chiappe, 1996). These changes are consistent with the inference that *M. ischiocaudalis* shifted off the ischial boot (see *Ischial Structures*, p. 153) onto the caudal portion of the pubic boot, becoming *M. pubocaudalis* on the line to birds. The so-called 'hypopubic cup' or 'spoon' (Ruben *et al.*, 1997; Martin *et al.*, 1998) of basal Avialae is the same as the caudal part of the pubic boot in other theropods (Norell & Makovicky, 1999). The test of congruence clearly indicates that these structures are synapomorphies of Neotheropoda + Herrerasauridae, and contrary morphological or phylogenetic data are lacking.

The ancestral degree of pubic retroversion for Eumaniraptora is similar (at or slightly past vertical; Ostrom, 1976a; Wellnhofer, 1985; Gauthier, 1986) and phylogenetically congruent (Serenó, 1999; Holtz, 2000). Homoplasy in the degree of pubic retroversion exists within Maniraptora, but this homoplasy does not falsify the homology of pubic retroversion for the clade Eumaniraptora. Many of the morphological differences among maniraptoran pubes are ancestral or derived character states, not non-homologous characters. The pubic symphysis and boot were lost as the pubes retroverted further within Alvarezsauridae and Pygostylia (Fig. 11; Chiappe, 1996; Hutchinson & Chiappe, 1998; also see Pubo-Ischiadic Plate, p. 141), assumedly in conjunction with changes in the PIFE and hypaxial musculature.

#### *Pubes and soft tissue anatomy*

Ruben *et al.* (1997, 1998, 1999) claimed that the similarities between crocodylomorph and theropod pubes, combined with controversial evidence of fossilized soft tissues, indicate that these two clades independently evolved a hepatic piston-based, diaphragmatically-ventilated lung. There are two main morphological problems with this scenario (also see Norell & Makovicky, 1999).

First, Ruben *et al.* (1998: 48) stated that crocodylomorphs and theropods "possess robust posterior gastralia and, in particular, a distinctive, tri-radiate pelvis that bears an elongate, spoke-like pubis". However, these structures are not independently derived but are ancestral for Archosauriformes (Benton & Clark, 1988). The pubes and ischia of archosaurs did independently become more separated as these elements elongated, the pubo-ischiadic plate reduced, and the pubo-ischiadic fenestra widened (see Pubo-Ischiadic Plate, pp. 137–142). Nevertheless, the 'tri-radiate pelvis' and 'robust posterior gastralia' are ancestral archosaurian features, not unique to Crocodylia (*contra* Ruben *et al.*, 1997: 1270). Most basal Archosauriformes have elongate pubes with extensive

aprons. In contrast, the crocodylian pubis is secondarily shortened relative to the ancestral suchian condition (Figs 8, 11–13; Benton & Clark, 1988; Russell & Wu, 1997).

Second, some of the pubic bone surface homologies assumed by Ruben *et al.* (1997, 1998, 1999) are untenable. Ruben *et al.* (1997: fig. 4a–d) compared crocodylian pubes with theropod pubes in lateral view, but these are not homologous lateral bone surfaces. The crocodylian bone surface shown is caudal, not lateral, and is occupied primarily by the origin of the PIFE2, not *M. diaphragmaticus* (Fig. 14; also see Pubo-Ischiadic Plate, pp. 145–146). I have observed that the attachment of *M. diaphragmaticus* to the craniolateral pubes is thin, fleshy, and not unambiguously indicated by any osteological correlates; the PIFE1 and 2 occupy most of the pubic apron surfaces.

As argued above, the crocodylian 'boot' is a vestige of the ancestral archosauriform pubic apron, not a craniocaudally expanded boot as in some theropods. Contrastingly, the pubic boot of Herrerasauridae and Tetanurae is an expansion of the lateral surface of the distal pubic symphysis, not the pubic apron *sensu stricto*. My examples illustrate the importance of an explicit phylogenetic approach to bone structure and surface homologies, and cast doubt on our ability to infer the presence of *M. diaphragmaticus* in any non-crocodyliform archosaur. The pubes are mobile in Crocodylia but are certainly immobile in theropods and most other non-crocodyliform archosauromorphs (except pterosaurs). Such mobile pubes may be correlated with the presence of *M. diaphragmaticus*, further weakening the inference that any theropods had such a ventilatory mechanism. Carrier and Farmer (2000) offer a much more reasonable reconstruction of archosaur pelvic anatomy, function, and evolution.

#### *Summary of pubic evolution*

The reduction of the pubic tubercle into a small rugosity reflects the reduction of the pubo-ischiadic ligament (and flexor cruris muscles) in basal Archosauriformes. As the pubic symphysis elongated into a large apron within Archosauriformes, the PIFE1 presumably shifted onto the cranial surface of the pubic apron, which the PIFI1 vacated as it shifted dorsally. The origins of *M. rectus abdominus* migrated off the reduced pubic tubercle and pubo-ischiadic ligament onto the distal pubic symphysis and the stout posterior gastralia. These derived traits were present in the ancestral archosaur. Basal theropods evolved a pubic boot related to modified hypaxial musculature, such as a partial shift of the origin of *M. ischiocaudalis* from the ischial boot onto the pubic boot. The obturator foramen became confluent with the pelvic and pubo-ischiadic fenestra within Tetanurae as the pubic apron reduced. The

**Table 5.** Taxonomic distribution of some ischial features discussed in the text

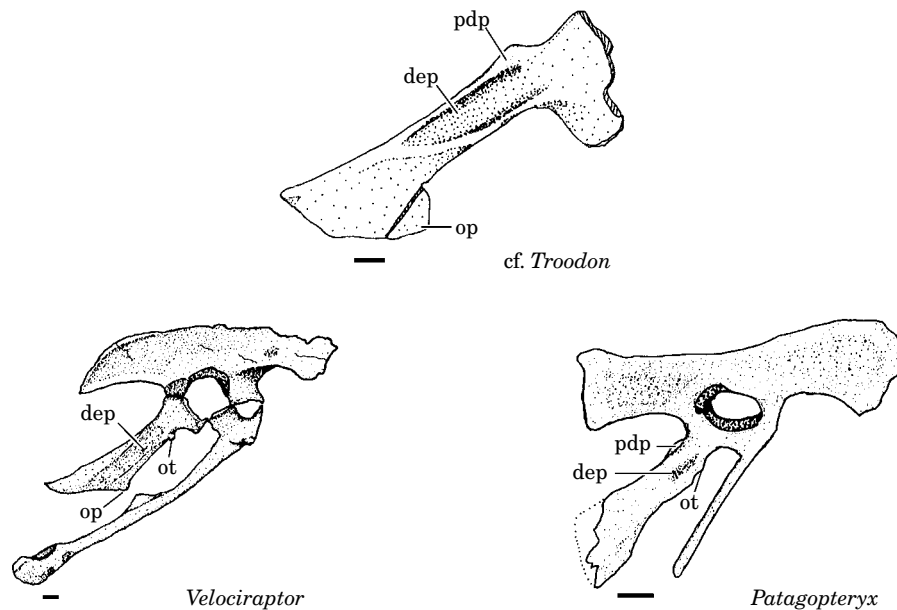
<p>A1. Large ischial tuberosity (Fig. 11: it): Basal Reptilia (Romer, 1956; Benton, 1983).</p>	<p>presence of a proximal dorsal process in <i>Patagopteryx</i> (MACN-N 03; fragment of a left ischium that was previously unidentified).</p>
<p>A2. Ischial tuberosity reduced to a slight rugosity (Fig. 11: it): Archosauriformes (Ewer, 1965; Cruickshank, 1972; Romer, 1972; Charig &amp; Sues, 1976; Weems, 1980), including Crurotarsi such as Parasuchia (<i>Rutiodon</i>, UCMP 119331, 119348; 32139), Aetosauria (Walker, 1961; <i>Stagonolepis</i>, UCMP 32148, 32153), Pposauridae (Chatterjee, 1985; DMNH 27724), and crocodylians (<i>Alligator</i>, UCMP 71672, 119043, 119045; <i>Caiman</i>, UCMP 63533, 123095, 132076; <i>Crocodylus</i>, UCMP 123090). Sauropodomorpha often have a scar in this location (Huene, 1926; <i>Patagosaurus</i>, MACN-CH 935), whereas the condition is uncertain in Ornithischia (but see Romer, 1927a). Among theropods, the scar is present in <i>Herrerasaurus</i> (MCZ 4381), <i>Coelophysis</i> (CMNH 10871), <i>Dilophosaurus</i> (UCMP 37302), <i>Sarcosaurus</i> (Andrews, 1921), <i>Ceratosaurus</i> (Gilmore, 1920), <i>Carnotaurus</i> (Bonaparte, Novas &amp; Coria, 1990), <i>Piatnitzkysaurus</i> (MACN-CH 895), <i>Afrovenator</i> (UCOBA 1), Carnosauria such as <i>Allosaurus</i> (AMNH 813, 5753) and <i>Acrocanthosaurus</i> (Harris, 1998), <i>Siamotyrannus</i> (Buffetaut <i>et al.</i>, 1996), <i>Ornitholestes</i> (AMNH 619), Tyrannosauridae and Ornithomimosauria (especially prominent; Holtz, 1994), <i>Deinonychus</i> (small but present on the caudodorsal ischium of YPM 5235), and most other non-avian taxa.</p>	<p>B1. Distal ischial tubercle (Fig. 11: dt) present: <i>Herrerasaurus</i> (Novas, 1994), <i>Afrovenator</i> (UCOBA 1), <i>Piatnitzkysaurus</i> (MACN-CH 895), <i>Allosaurus</i> (AMNH 680, 813, 5753; MOR 693; USNM 2323), <i>Giganotosaurus</i> (MUCPv-CH 1), <i>Acrocanthosaurus</i> (Harris, 1998), <i>Sinraptor</i> (a crest; Currie &amp; Zhao, 1994), and Therizinosauroida (Barsbold, 1983).  B2. Distal dorsal process of the ischium (Fig. 11: ddp) present: <i>Sinornithosaurus</i> (Xu <i>et al.</i>, 1999), Rahonavis, <i>Archaeopteryx</i>, Confuciusornithidae, and other Avialae (Zhou, 1995a,b,c; Forster <i>et al.</i>, 1998; Martin <i>et al.</i>, 1998).</p>
<p>A3. Ischial tuberosity extended into a proximal dorsal process of the ischium (Figs 11, 15: pdp): Tyrannosauridae (CM 9380; MOR 555; ROM 807, 1247; RTMP 81.10.1, 91.36.500), cf. Maniraptora; possibly a deinonychosaur (RTMP 86-77-2), <i>Sinornithosaurus</i> (Xu <i>et al.</i>, 1999), <i>Unenlagia</i> (Novas &amp; Puerta, 1997), <i>Archaeopteryx</i> (Ostrom, 1976a), <i>Rahonavis</i> (Forster <i>et al.</i>, 1998), and other extinct Avialae (Sanz, Chiappe &amp; Buscalioni, 1995; Zhou, 1995a,b,c; Martin <i>et al.</i>, 1998). I have also discovered the</p>	<p>C1. Obturator tuberosity ('processus obturatorius') present (Figs 11, 15, 16, 18: ot): <i>Deinonychus</i> (YPM 5235), <i>Velociraptor</i> (Norell &amp; Makovicky, 1997), <i>Troodon</i> (MOR 553L and 553S), and the alvarezsaurid <i>Shuvuuia</i> (IGM 100/99). A corresponding tubercle (for pubo-ischiadic ligament attachment) is present on the pubic shaft of <i>Sinornithosaurus</i> and other deinonychosaurs (Xu <i>et al.</i>, 1999). In birds it is present in <i>Concornis</i> (Sanz <i>et al.</i>, 1995), <i>Chaoyangia</i> (Zhou, 1995a), <i>Patagopteryx</i> (Chiappe, 1996; MACN N 11), Ichthyornithiformes (Marsh, 1880; Zhou, 1995a), and Neornithes (many MVZ and UCMP specimens).</p>
<p>pubic boot expanded until Maniraptora, when it reduced as the pubes retroverted (corresponding to further modifications of abdominal muscles). The pubic tubercle became more spinelike in Eumaniraptora. The pubic boot was eventually lost in <i>Patagopteryx</i> + Ornithurae as the pubes and ischia became even more retroverted. When the pubic apron was lost in these birds, perhaps the PIFE2 moved caudomedially into its position as the OM, and the PIFE1 became the tiny OL.</p>	<p>D1. Medial ridges on the pubes and ischia (Fig. 17: cr, mr) for the attachment of a pubo-ischiadic membrane: <i>Torvosaurus</i> (BYU 2014), <i>Marshosaurus</i> (UUVP 40-295, 4736), <i>Allosaurus</i> (Madsen, 1993; AMNH 704), <i>Albertosaurus</i> (AMNH 5218), <i>Archaeornithomimus</i> (AMNH 21798, 21799), <i>Microvenator</i> (AMNH 3041), <i>Velociraptor</i> (IGM 100/985), <i>Patagonykus</i> (Novas, 1997), <i>Rahonavis</i> (UA 8656), and many other tetanuran taxa.</p>

#### ISCHIAL STRUCTURES

##### *Ischial tuberosity*

Reptilia ancestrally has an angular dorsal process of the proximal ischium, or ischial tuberosity (Fig. 11: it;

Romer, 1956), that is similar to the pubic tubercle. Chelonia modified this structure into a 'metischial process' that may contact the plastron but ancestrally retains its soft tissue attachments (see Pelvic Ligaments, pp. 158–159). The homologue of the FTI3 (confusingly termed the FTI2 in more basal Reptilia) originated from the ilio-ischiadic fascia or ligament (close to the tuberosity) ancestrally in Reptilia (Gadow, 1882a; Romer, 1922, 1923b). The ischial tuberosity of basal Reptilia also is the origin of *M. ischiocaudalis*, as well as the attachment of the pubo-ischiadic and ilio-ischiadic ligaments. It is present in basal archosauriforms, but in Archosauriformes it is reduced (Table 5A) to a round scar or tubercle on the caudolateral surface of the proximal ischium. This rugosity is near the iliac peduncle, in the same position as the



**Figure 15.** Ischial structures in Maniraptora. Right elements in lateral view: right ischium of cf. *Troodon* (Maniraptora; TMP 86-77-2), and pelvis of *Velociraptor* (left pelvis of IGM 100/985, reversed) and *Patagopteryx* (reconstructed based on MACN-N 03 and 11). Scale bar = 1 cm.

ischial tuberosity of more basal Reptilia. It is not present in more basal archosauriforms or other Reptilia that have the ischial tuberosity; thus homologizing these features is unproblematic.

The ischial tuberosity marks the tendinous origin of *M. flexor tibialis internus 3* (FTI3) in Crocodylia and is associated with ilio-ischiadic fascia (see Pelvic Ligaments, p. 159). Thus the ischial tuberosity of Archosauriformes may have ancestrally served as the origin of the FTI3 (*vide* Romer, 1923b) as well as an attachment for reduced pelvic ligaments and fascia. *M. ischio-caudalis* does not originate from the ischial tuberosity in Crocodylia; its attachment is on the distal end of the ischium. Reduction of the ischial tuberosity in Archosauriformes, then, is correlated with a shift of *M. ischio-caudalis* onto the distal ischium and a shift of the FTI3 onto the ischial tuberosity as the pelvic ligaments were reduced. This sequence is similar to changes of the pubic tubercle and its associated soft tissues.

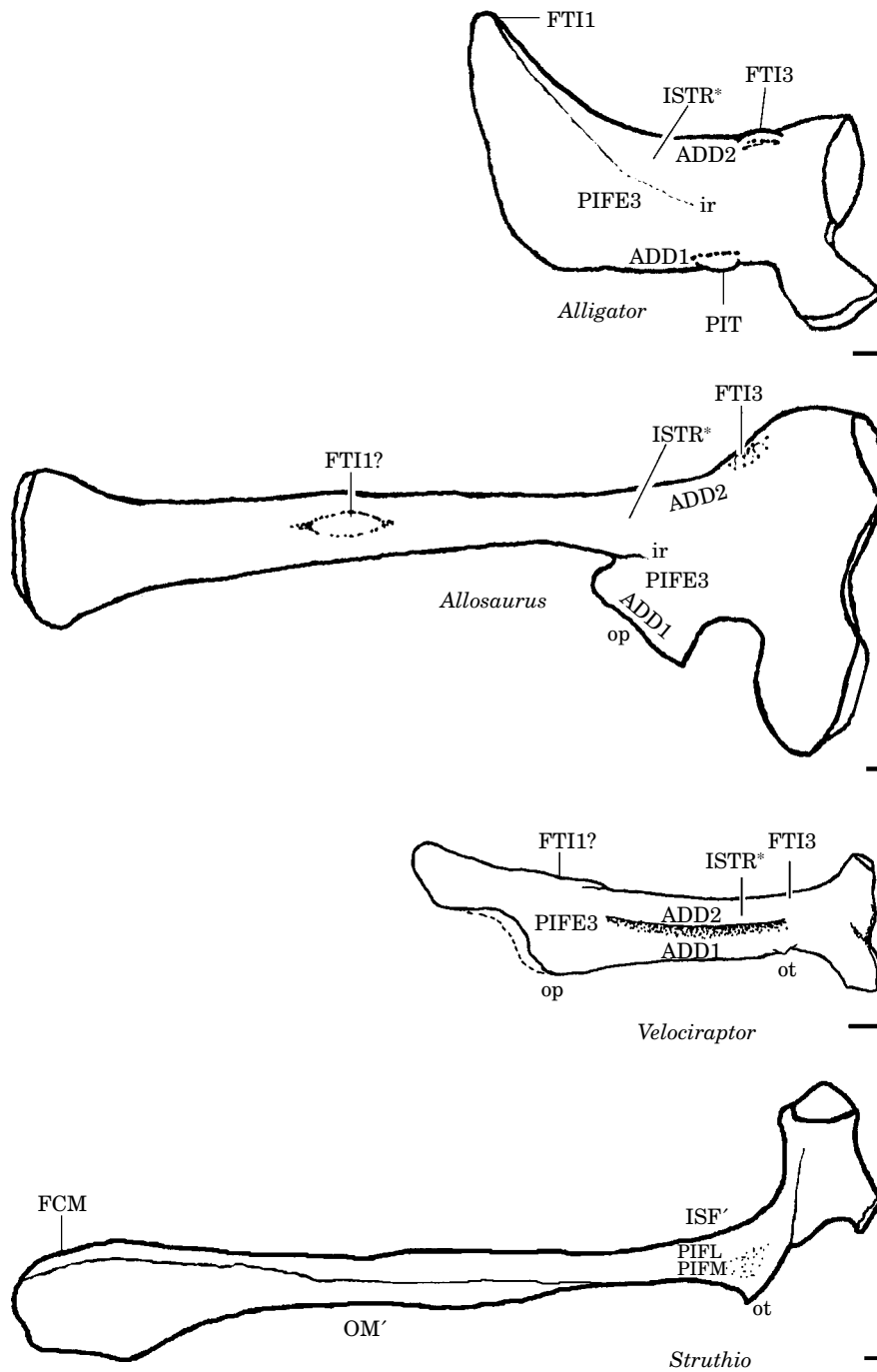
I have not seen an identical ischial rugosity in any birds. However, a proximal dorsal process of the ischium (Figs 11, 15: pdp) is present as an expansion of the ischial tuberosity in many Coelurosauria, including birds (Table 5A). The process is absent in Hesperornithiformes (Chiappe, 1996) and Paleognathae, although a similar process is present in some Neognathae (*pers. observ.*). The proximal dorsal process is present in many taxa that lack the ischial tuberosity, and some specimens of tyrannosaurids (Table 5A) and crocodylians (e.g. *Caiman*, MACN-AC 1) may convergently develop the scar into a process. I infer that

the proximal dorsal process is a derived character state of the character 'ischial tuberosity'. The presence of an ischial tuberosity that is expanded into a proximal dorsal process is ancestral for Aves.

*M. flexor cruris medialis* (FCM; = FTI3 of Crocodylia; Romer, 1942) originates from the caudolateral surface of the distal ischium, not from an ischial tuberosity, requiring a slight distal shift of the FCM origin on the line to Neornithes (Fig. 16). The proximal dorsal process likely was the attachment for an ilio-ischiadic membrane (see Pelvic Membranes, pp. 154–156). Also, the proximal dorsal process may have formed as *M. ischio-trochantericus* (ISTR) moved its origin laterally from the medial surface of the ischium onto the lateral surface of the ilio-ischiadic membrane (see Pelvic Membranes, p. 156). All of these hypotheses require more data from basal birds and their outgroups in order to test them more rigorously.

#### *Distal ischial tubercle and distal dorsal process*

Another ischial tubercle or scar is present on the caudolateral surface of the distal ischium (Fig. 11: dt) in many theropods (Table 5B). However, I have not seen this tubercle in some other Theropoda. It is also not known in non-theropodan archosaurs, including crocodylians, basal ornithomirans, and basal dinosaurs (but the sauropod *Volkheimeria* has a similar tubercle; Bonaparte, 1979). The tubercle is absent in most Maniraptora, which have distally reduced ischia (Gauthier, 1986; Holtz, 1994; Chiappe, 1996). The tubercle fails



**Figure 16.** Archosaur ischial musculature. Right ischia in lateral view: *Alligator* (UCMP 138037), *Allosaurus* (reconstructed based on AMNH 5753), *Velociraptor* (reconstructed based on the left ischium of IGM 100/985, reversed), and *Struthio* (left ischium of UCMP 9349, reversed). See Table 1 for muscle abbreviations. The ISF' (= ISTR) originates mainly from the nearby ilio-ischiadic membrane, whereas the OM' originates mainly from the medial surface of the pubo-ischiadic membrane. Abbreviations ending in an asterisk (\*) originate medial to the point indicated (i.e. behind the surface shown). Scale bar = 1 cm.

the test of conjunction with the ischial tuberosity (both are present in *Afrovenator*, *Allosaurus*, *Acrocanthosaurus*, and other Theropoda); those two structures are not variations of the same character.

The theropodan distal ischial tubercle is in a similar position as the M. flexor tibialis internus 1 (FTI1) origin in Crocodylia (Fig. 16), which has a faint scar. If the distal tubercle were indicative of the FTI1 origin,

its loss in Maniraptora would correspond to the loss of that muscle inferred in Neornithes (Romer, 1923b, 1927b).

Many Avialae (Table 5B) have a distal dorsal process of the ischium in a similar position (Fig. 5: ddp), as does the basal deinonychosaur *Sinornithosaurus* (Xu, Wu & Wu, 1999). The distal ischial tubercle and the distal dorsal ischial process could be different character states of the same character, yet that hypothesis is not congruent with available data. More data on these features are needed to resolve their homologies.

Assuming that the distal dorsal ischial process is not homologous with the distal ischial tubercle, the origination of the former structure could relate to a distal shift of the origin of the FTI3 (=FCM) off the proximal dorsal ischial process. Many alternative scenarios are feasible; I favour the preceding one because it is the most consistent with available data. The history of the flexor cruris muscle group remains poorly understood. Fossils do not yet clarify its homologies, but offer hope of an eventual resolution.

#### *Obturator process*

The ischial obturator process (Figs 8, 10, 11, 15, 16: op) of some archosaurs is a source of confusion in the literature (e.g. Romer, 1927a; Thulborn, 1972; Santa Luca, 1984; Gauthier, 1986; Sereno, 1991b; Novas, 1996). This confusion stems from a lack of clear consensus on what an obturator process is, what it evolved from, how many times it evolved, and what its significance for soft tissue evolution might be. I follow Novas (1996: 734) in defining the obturator process as a laterally concave cranioventral keel on the ischium, often proximally positioned (at least in basal taxa). It is a derivation of plesiomorphic pubo-ischiadic plate bone surface, i.e. a part of the ischial 'apron' (=expanded symphysis). It is plesiomorphically connected to the proximal pubo-ischiadic symphysis, forming the continuous ventral margin of the pelvic canal (Fig. 8B).

The obturator process became proximally located on the ischium by the caudoventral elongation of the distal ischiadic symphysis into an ischiadic apron (see Pubo-Ischiadic Plate, p. 141), e.g. within Dinosauriformes. It is not identifiable as a distinct anatomical structure until arising (at least once) within Ornithischia and Tetanurae—basal Dinosauriformes lack a distinct obturator process. The cranioventral corner of the ischium in Crocodylia (and some other Suchia) could be considered an 'obturator process', although it is not as distinct as the processes that evolved within Dinosauria.

In Avetheropoda the obturator process is quite distinct and oddly shaped, but it is still a remnant of the pubo-ischiadic plate. It is not yet resolved how this

region of the pubo-ischiadic plate became a pronounced cranial process (i.e. a true obturator process) in Avetheropoda (Charig & Milner, 1997; Holtz, 2000). The obturator process probably became conspicuous after the loss of the ventral boundary of an ischial foramen, much like the pubic obturator foramen or notch (see Martill *et al.*, 2000). The loss of the ventral boundary of the ischial foramen would have connected the opening with the pelvic fenestra (cranially) and the pubo-ischiadic fenestra (ventrally). Ischial foramina are known in some basal theropods such as *Segisaurus* (UCMP 32101), *Monolophosaurus* (Zhao & Currie, 1994), and possibly *Yangchuanosaurus* (Currie & Zhao, 1994), but character optimizations do not currently favour these foramina as ancestral for Tetanurae.

The obturator process remained distinct in Coelurosauria, but was reduced and distally located on the shortened ischium in Maniraptora (Figs 8B, 11, 15, 16; Gauthier, 1986; Holtz, 1994) as the ischial apron was reduced distally and the pelvis widened. When the ischiadic symphysis split up in Aves, the obturator process was reduced to the cranioventral corner of the distal ischium (Ostrom, 1976a; Forster *et al.*, 1998). The obturator process was 'lost' (or at least became indistinct from the remainder of the ischium) once ischial contact was lost in Pygostylia (Chiappe, 1996; Novas, 1997; Sereno, 1999). Thus the last vestige of the ischial portion of the pubo-ischiadic plate was lost in Pygostylia.

Changes of the obturator process have implications for the evolution of several ventral pelvic muscle groups (Fig. 16). *M. adductor femoris 1* (ADD1) is also present on the cranioventral edge of the crocodylian 'obturator process' (Romer, 1923b). The origin of its neornithine homologue (*M. pubo-ischio-femoralis medialis*; PIFM) is in a topologically similar position. If the crocodylian ADD1 origin is plesiomorphic for Archosauria (see Pelvic Ligaments, p. 158), then its avian homologue (the PIFM) would have shifted off the obturator process onto the cranial edge of the ischial shaft as the latter was reduced in Pygostylia and the PIFE3 was lost.

The ischial ridge (Figs 8, 16: ir; see Pubo-Ischiadic Plate, p. 137) is cranioventral to the ischial scar for *M. flexor tibialis internus 3* (FTI3). It is ventral to a second scar or groove that lies distal to the FTI3 scar, on the caudal edge of the ischium. This second scar corresponds to the main part of the ADD2 origin. The homology of the ischial ridge and scar among archosauriforms suggests that the ADD2 (= *M. pubo-ischio-femoralis lateralis* [PIFL] of Neornithes) was ancestrally present in archosaurs and their close relatives. This supports Romer's (1923b) hypothesis that the two heads of that muscle in birds and crocodylians are homologous.

It is not clear when the ADD2 (=PIFL) muscle origin shifted cranially to lie close to the first head on the

cranioventral ischium, as it does in Neornithes but not in Crocodylia (Figs 2, 16). A depression (Figs 15, 16: dep) between the ischial ridge and the caudal edge of the ischium in some archosaurs (e.g. some Ornithischia [Romer, 1927a: 249], deinonychosaurs such as *Deinonychus* [YPM 5235] and *Velociraptor* [Norell & Makovicky, 1997], and *Patagopteryx* [MACN-N 03, 11]) may corroborate the presence of the ADD2 origin here. The evolution of the 'obturator tuberosity' could relate to this change (see below).

The PIFE3 originates from the lateral surface of the ischial part of the pubo-ischiadic plate ancestrally in Reptilia (Romer, 1922, 1923b, 1956), and presumably from the obturator process in Avetheropoda. It lies between the ADD1+2 on the lateral surface of the ischium in Crocodylia (Fig. 16). Because Neornithes lack any evidence of having the PIFE3 (Romer, 1927b; Fig. 16), the PIFE3 may have been lost with the obturator process in Pygostylia.

Finally, the loss of the obturator process and ischial symphysis as well as the formation of the ilio-ischiadic membrane within Maniraptora is significant. These changes may correlate with the shift of the origin of *M. ischiotrochantericus* (ISTR) from the medial surface of the ischium onto the lateral surface of the ischium and the ilio-ischiadic membrane (Fig. 16; see Pelvic Membranes, p. 156).

#### *Obturator tuberosity*

Neornithes and many basal birds (Table 5C) have a structure called an 'obturator process' (processus obturatorius *sensu* Baumel & Witmer, 1993; here referred to as the obturator tuberosity). This feature (Figs 11, 15, 16: ot) is at the tip of a bony shelf that looks 'stretched' cranioventrally from the caudodorsal ischium across the lateral surface of the rodlike ischial shaft, giving the ischium a more flattened, less rodlike shape. The tuberosity is on the cranial edge of the proximal ischium, with a corresponding tubercle often opposite it on the pubic shaft. It appeared after the original avetheropodan obturator process was reduced (see above).

A small tubercle is proximal to the obturator process on the cranial edge of the ischium of some non-avian Maniraptora (Table 5C). Considering its similar structure and position in these outgroups to Aves, this tubercle appears to be the same as the 'avian' obturator tuberosity. The presence of the obturator tuberosity may be a eumaniraptoran synapomorphy. Assuming that the maniraptoran proximal ischial tubercle is indeed an obturator tuberosity, the obturator process and obturator tuberosity do not pass the test of conjunction (both processes are present in some maniraptorans). In any case, the homology of the 'avian' obturator tuberosity with the avetheropodan obturator

process is not supported because it does not pass the test of congruence (the true obturator process shifted distally and was lost in Pygostylia).

In Neornithes the obturator tuberosity is indicative of the attachment of the ligamentum ischiopubicum (Baumel & Raikow, 1993). This ligament forms the ventral boundary of the obturator foramen and the dorsal boundary of the pubo-ischiadic membrane (see Pelvic Membranes, pp. 154–155). The ligamentum ischiopubicum also forms a pulley for constraining the line of action of the tendon of the OM (=PIFE2; see p. 146), preventing the tendon from moving distally. The presence of the obturator tuberosity and its ligament indicates that the OM tendon exited proximally through the obturator notch, as in Neornithes, rather than running straight from the pubic apron, as in Crocodylia (Fig. 14). Thus the presence of the obturator tuberosity reflects a cranioventral shift of the ischial attachment point of the pubo-ischiadic ligament (see Pelvic Ligaments, p. 158). If this hypothesis of homology is correct, that change may also correlate with the cranioventral shift of the ADD2 (=PIFL) origin on the line to Neornithes (see Obturator Process, p. 152). The result would be that the ADD2 muscle origin moved close to the ADD1 (=PIFM) as the PIFE3 between these two adductor muscles reduced.

Although more data from basal avialans are needed to further test my hypothesis of homology, there seem to be no viable alternative hypotheses for the identity of the obturator tuberosity. Crocodylia have a scar for the origin of *M. pubo-ischio-tibialis* (PIT) that is similar in position to the tuberosity (e.g. *Caiman*, MACN-AC 1; Fig. 16). However, all basal archosaurs through basal maniraptorans lack such a scar, and thus the similarity must be seen as homoplasy (*contra* Romer, 1923c). There is no evidence for any dinosauromorph having one or more parts of the PIT; perhaps that muscle was lost within Dinosauromorpha.

#### *Ischial boot and retroversion*

Finally, the distal ischium of Neotheropoda ancestrally ends in an expanded 'boot' similar to the pubic boot (Fig. 11: ib; Gauthier, 1986; Holtz, 2000). Like the pubic boot (see Pubic Structures, p. 146), it is an expansion of the lateral bone surface, and it probably anchored hypaxial musculature (e.g. *M. ischiocaudalis* and *M. rectus abdominus*), as well as pubo-ischiadic connective tissue.

The ischium reduced distally in coelurosaurs, losing the boot within Maniraptoriformes (Holtz, 2000). This reduction occurred as the ischium shortened relative to the rest of the pelvis and the obturator process became distally situated (Chiappe, 1996). Loss of the ischial boot may indicate more concentration of the origin of *M. ischiocaudalis* (= *M. pubocaudalis* of Aves)

on the caudal part of the pubic boot rather than on the ischium. The ischia secondarily elongated in Ornithurae (Chiappe, 1996) and within Alvarezsauridae (Hutchinson & Chiappe, 1998; Chiappe *et al.*, 1996). This secondary elongation occurred as the pubes and ischia retroverted more and the pelvis widened further.

In many respects, the evolution of the ischium proceeded in advance of similar changes in the pubes, such as forming or reducing the boot, widening the pelvis, and splitting the symphysis. Reasons for this pattern are not yet clear, but it is interesting to note that a similar pattern predominates dorsally: the anterior synsacrum remained relatively narrow as the posterior synsacrum broadened greatly within Eumaniraptora, especially Ornithothoraces.

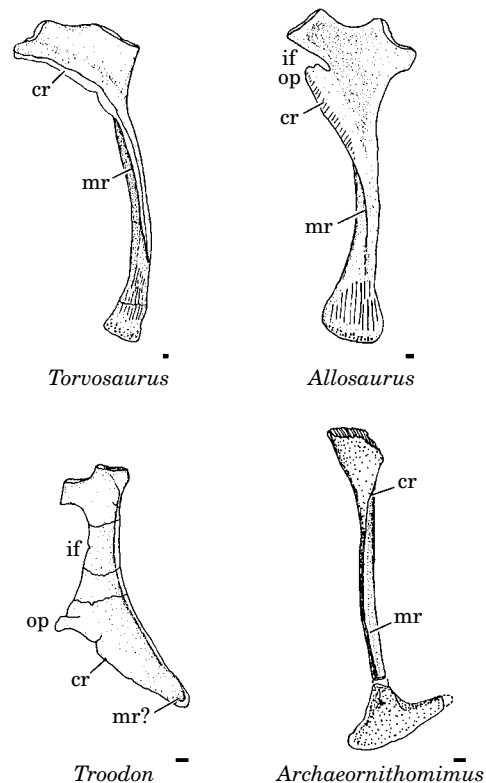
#### Summary of ischial evolution

Like the pubic tubercle, the ischial tuberosity reduced to a rugosity within Archosauriformes, signalling changes of the pelvic ligaments and FTI musculature. Like the pubic boot, the ischial boot of Neotheropoda indicates modification of hypaxial musculature. As the ischium was reduced distally within Maniraptora, the ischial boot was lost (entailing more modifications of abdominal muscles) and the obturator process assumed a more distal position (further reducing the ischial apron). Eumaniraptora evolved an obturator tuberosity (proximal to the obturator process) that was associated with a modified pubo-ischiadic ligament and PIFE2. The ADD2 origin moved cranially to lie appressed to the ADD1 as the PIFE3 was reduced with the obturator process. Avialae modified the ischial tuberosity into a proximal dorsal process that was associated with positional shifts of several soft tissues (possibly including the ISTR, the FTI3, and an ilio-ischiadic ligament or membrane). Basal birds also evolved a distal dorsal ischial process and eventually lost the obturator process and ischial sympysis. Finally, in Ornithurae the ischia elongated and became well retroverted.

#### PELVIC MEMBRANES

##### *Pubo-ischiadic membrane*

A fibrous membrane called the pubo-ischiadic membrane occupies the ventral space between the ischia and pubes (thyroid or pubo-ischiadic fenestra) in extant Reptilia. Considering its similar position in extant taxa, this membrane might seem to be homologous among these taxa. However, fossils reveal that the pubo-ischiadic plate opened independently into thyroid or pubo-ischiadic fenestrae in the ancestors of Chelonia, Lepidosauria, Crocodylia, and Neornithes (Figs 8, 10, 11). Because the feature arose independently at least four times it should be regarded as a reptilian



**Figure 17.** Medial ridges of the ventral pelvis in theropod dinosaurs. Elements in medial view: right ischia of *Torvosaurus* (basal Tetanurae; BYU 2015), *Allosaurus* (Carnosauria; left ischium of AMNH 813, reversed), and cf. *Troodon* (Maniraptora; MOR 553L); and right pubis of *Archaeornithomimus* (Ornithomimidae; AMNH 21798). In both the pubis and ischium, scarred ridges on the ventral pelvic elements begin proximally as a cranial ridge that distally becomes a more medial ridge. 'cr' is the cranial ridge, 'if' is the ischial fenestra (opening into the pelvic fenestra/pelvic canal), and 'mr' is the medial ridge. Scale bar = 1 cm.

parallelism (*sensu* Patterson, 1982): it passes the test of similarity but not the test of congruence. The four independent originations of this structure correspond to several differences in ventral pelvic musculature (e.g. the PIFI and PIFE) and routes taken by N. obturatorius through this region among these clades.

The pubo-ischiadic membrane extends from the medial edge of the pubes to the cranial ischium in Crocodylia. It passes from the caudal edge of the pubes to the cranial ischium in Neornithes, and ossifies in some adults. Indeed, the membrane could be seen as unossified pubo-ischiadic plate surface or mesenchyme, depending on how loosely one interprets the test of similarity. Like the pelvis of living archosaurs, fossil archosauriform pelvis have ligamentous scarring on the edges of the pubo-ischiadic fenestra that correspond to the attachments of the membrane (Fig. 17).



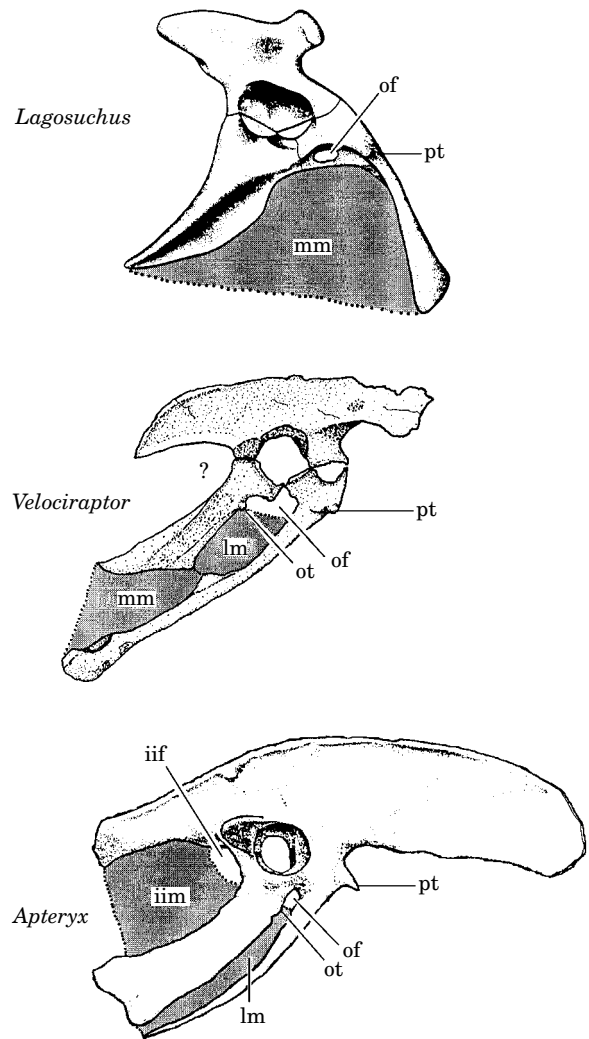
I infer that a pubo-ischiadic membrane spanned the pubo-ischiadic fenestra (when present) in extinct archosauromorphs. The membrane is present in living Archosauria, and extinct taxa have osteological correlates that are consistent with the presence of such a membrane. It was plesiomorphically absent in Archosauromorpha, but formed and expanded as the pubo-ischiadic fenestra formed. However, some osteological correlates indicate that this membrane evolved differently on the lines to Crocodylia and Neornithes.

The rugose scarring on basal archosauriform pelvis, including basal Crurotarsi and Ornithodira, is near the body midline, following the ventral pelvic symphyses. This scarring suggests the presence of a single medial (sagittal) membrane ancestrally in Archosauria. The ventral symphyses split independently on the lines to Crocodylia and Neornithes (see Pubo-Ischiadic Plate, pp. 138–142). As the hips widened and these symphyses ‘unzipped’, so would have the single medial membrane, producing the two lateral membranes on either side of the body in living Archosauria (Fig. 18: mm, lm). This is the least speculative evolutionary scenario, but such a hypothesis would not be very parsimonious if data from fossil outgroups were ignored. Two sources of evidence from fossil theropods corroborate this hypothesis.

First, the pubic shaft has a proximodistal ridge that runs from the caudal surface of the proximal pubis (near the obturator foramen or notch) to the medial surface of the pubic apron. This ridge is present in most Tetanurae (Table 5D). A matching ridge runs from the cranial to medial edge of the ischium (Fig. 17: cr, mr). These ridges extended distally as the pubic and ischial apron reduced distally and the pelvic canal was opened ventrally (see Pubo-Ischiadic Plate, p. 137). It remained as the thin caudal edge of the pubis once the pubic symphysis and apron were lost in *Patagopteryx* + Ornithurae. The caudal and cranial edges of the pubes and ischia are particularly rugose distal to the obturator tuberosity in *Patagopteryx* (Fig. 15; Chiappe, 1996; MACN-N 03), suggesting the presence of a continuous lateral membrane spanning the space between them (as in Neornithes).

A second line of evidence is that the obturator process of the ischium and the caudal tip of the proximal pubic apron (the obturator notch) point toward each other in articulated tetanuran pelvis (Figs 8B, 11, 15), even fusing in some Therizinosauroidea (Barsbold, 1983). This implies a soft tissue connection between them after their bony symphysis was lost within Tetanurae.

Together these data suggest that a lateral membrane was present proximal to the pubic apron and obturator process, and the ancestral sagittal membrane was maintained distally until the symphyses split apart. Because the breakup of the pubic symphysis lagged



**Figure 18.** Pelvic membrane morphology reconstructed for *Lajosuchus* (Dinosauriformes; modified from Sereno & Arcucci, 1994), *Velociraptor* (Deinonychosauria; left pelvis of IGM 100/985, reversed), and *Aapteryx* (Paleognathae; modified from McGowan, 1979). Shaded areas are reconstructed membranes; dotted lines are membrane boundaries. ‘iim’ is the ilio-ischiadic membrane, ‘lm’ is the lateral membrane, and ‘mm’ is the medial membrane. ‘?’ indicates that ‘iim’ formation is possible, but equivocal. Scaled to the same pelvic height.

behind the splitting of the ischial symphysis (see pp. 141, 152–153), the lateral membranes may have been more distinct caudodorsally in basal Avialae, forming a cranially pointing ‘V’ (Fig. 18).

The evolution of the pubo-ischiadic membrane is important for understanding pelvic muscle evolution. Chelonia and Lepidosauria have the PIFI (medially) and PIFE (laterally) originating from this area (as in Reptilia ancestrally), whereas Crocodylia has only a tiny PIFE3 subdivision originating there (laterally;

Fig. 14B), and Neornithes has the OM origin occupying most of the membrane (medially; Fig. 14D). I infer that the PIFE2 shifted caudomedially onto the medial surface of the membrane to become the derived OM of Neornithes (see Pubic Structures, p. 146) in *Patagopteryx* + Ornithurae.

#### *Ilio-ischiadic membrane*

An ilio-ischiadic membrane (Fig. 18: iim, 19: iil) is present in the caudal end of the ilio-ischiadic fenestra of Neognathae and in the same region in Paleognathae. It spans the space between the ventrolateral edge of the lamina infracristalis ilii and the caudodorsal edge of the ischium. An ilio-ischiadic ligament (see pp. 158–159) is present in some Reptilia in the same relative position. N. ischiadicus passes through the cranial end of the ilio-ischiadic fenestra in neognaths, identical to its position in Paleognathae and reptilian outgroups. Neognath birds have an ilio-ischiadic fenestra (Figs 11, 18: iif; Cracraft, 1986; Baumel & Witmer, 1993) that would appear to be unique to Neognathae. However, this structure is also present in some Enantiornithes (Walker, 1981; Zhou, 1995a,b; Chiappe, 1996), and the fenestra is almost closed in many Paleognathae (pers. observ.) and other Ornithothoraces (Zhou, 1995a,b). Chatterjee (1997, 1998) alleged that *Protoavis* has an ilio-ischiadic fenestra, but based on my examination of TTU P 9200, I am not convinced that the bones are avian or even pelvic. Nonetheless, homoplasy appears to be abundant in this region within Aves.

I concur with Zhou (1995a,b) that the evolutionary precursors of the ilio-ischiadic membrane are visible in fossil Maniraptora, especially within Aves. The two dorsal processes of some eumaniraptoran ischia (see Ischial Structures, pp. 148–152) may indicate the attachments of an ilio-ischiadic membrane or its precursor. Martin *et al.* (1998: 287–288, fig. 2k) stated that the proximal dorsal process of the ischium of *Archaeopteryx* and *Confuciusornis* is “abutting against the ilium”. This is not evident from their reconstructions, other published information, or specimens that I have seen (except for one enantiornithine; Fig. 6). Nevertheless, the proximity of the proximal dorsal process to the ventral rim of the ilium may indicate that soft tissues connected these structures. The ventral curvature of the postacetabular ilium, reduced brevis fossa, and increased retroversion of the ischia in some Maniraptora (Gauthier, 1986; Novas, 1997; Carrano, 1998) may also signal the incipient formation of the ilio-ischiadic fenestra. Additional basal maniraptoran fossils should clarify how this transition occurred.

M. ischiotrochantericus (ISTR; = M. ischiofemoralis or ISF of Aves) originates from the medial surface of

the ischium ancestrally in Reptilia (Gadow, 1882a; Romer, 1922, 1923b), but the ISF originates from the lateral surface of the ischium and ilio-ischiadic membrane in Neornithes (Fig. 2). The origin of the ISTR probably shifted laterally as the ilio-ischiadic membrane formed and the ischial apron was reduced (with ischial retroversion) within Maniraptora (Fig. 18). The origin may have shifted onto the lateral surface of the proximal dorsal process as the FTI3 moved off the ischial tuberosity (Fig. 16) and the pubo-ischiadic ligament shifted position with the obturator tuberosity. This change would have produced the derived ‘neornithine’ origin of the ISF.

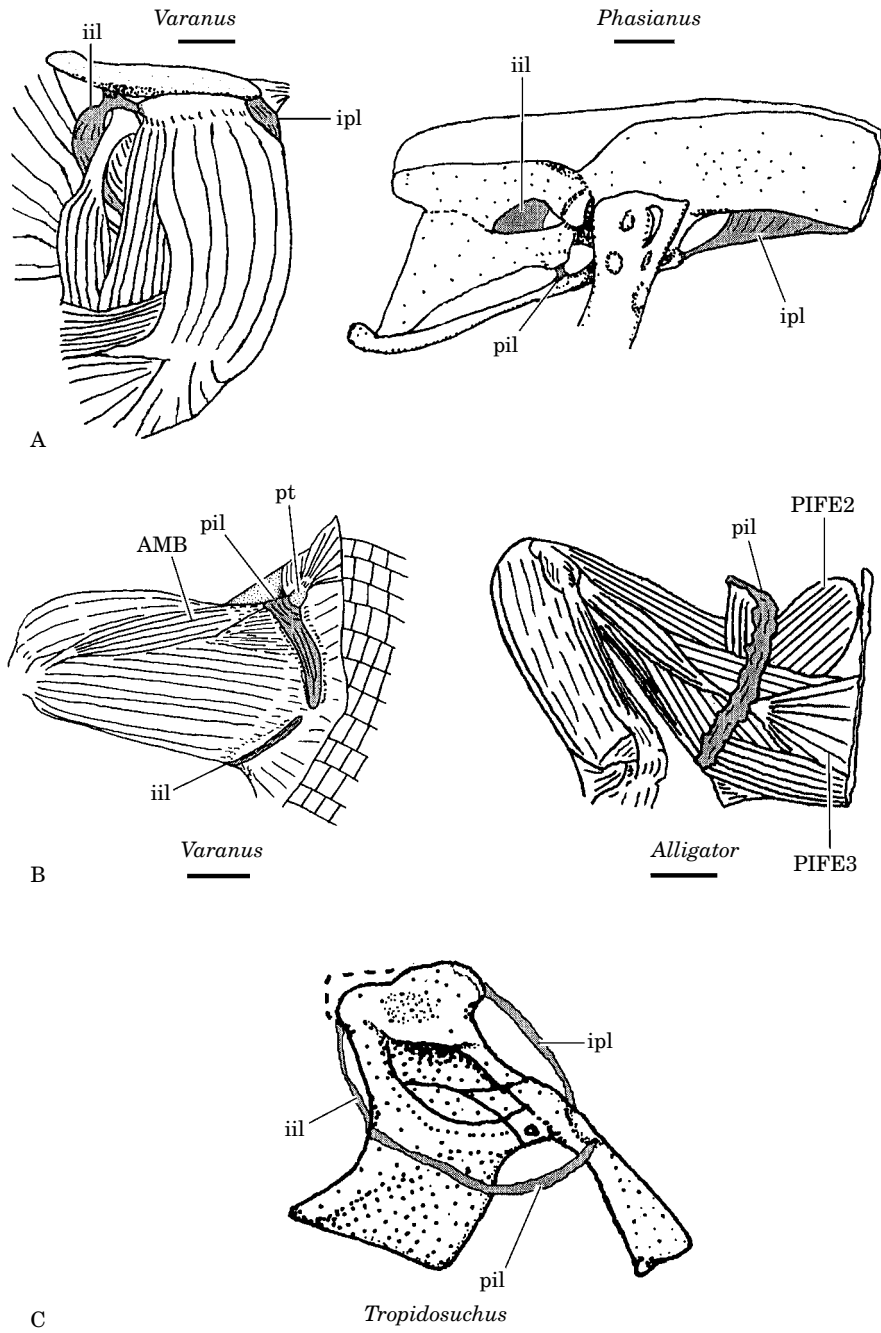
Note that the CFB (=CFP of Aves) origin must have moved fully laterally before the ilio-ischiadic membrane formed; otherwise it would have been trapped medial to the membrane (cf. Figs 2, 18). Because the brevis fossa was reduced or lost in Eumaniraptora, the ilio-ischiadic membrane may have formed within Eumaniraptora after the CFB origin moved laterally to become the CFP. The convergent evolution of a brevis fossa-like structure in some birds probably relates to modifications of ilio-ischiadic membrane attachments rather than the CFP. Again, the widening of the pelvis, the reduction of the brevis fossa, and other osteological and muscular changes in the ilio-ischiadic region seem to have been part of a complex series of soft tissue reorganizations before and during the evolution of avian flight.

#### PELVIC LIGAMENTS

A series of ligaments and fascia forming a semicircle around the ventrolateral pelvis is present in extant Reptilia (Figs 18, 19). These ligaments serve as thigh muscle origins, support muscles and other soft tissues, and act as pulleys to change the lines of action of muscles. The ligaments are closely associated with nearby muscles and are often difficult to differentiate from the aponeuroses and tendons of attached muscles. Pelvic ligaments are of interest because their modifications correspond to alterations of the muscles that ancestrally attached to them. Romer (1922, 1923b, 1956) considered the ilio-pubic ligament, pubo-ischiadic ligament, and ilio-ischiadic ligament to have been ancestral reptilian features that were lost in archosaurs. This assertion may be viewed differently when explicitly framed in a phylogenetic context that includes fossils.

#### *Ilio-pubic ligament*

An ilio-pubic ligament (Fig. 19: ipl) is clearly present in Lepidosauria and Neornithes (the ligamentum inguinale *sensu* Baumel & Raikow, 1993: 174). It connects the cranioventral preacetabular ilium to the pubic tubercle (=preacetabular tubercle of Aves) and serves



**Figure 19.** Pelvic ligament morphology (from my dissections). A, *Varanus* (on left) and *Phasianus* (on right) pelvises in lateral view. B, *Varanus* (on left) and *Alligator* (on right) pelvises in ventral view. C, pelvic ligaments reconstructed for *Tropidosuchus* (Proterochampsidae; right pelvis of PVL 4601 in lateral view). 'iil' is the ilio-ischiadic ligament (or membrane), 'ipl' is the ilio-pubic ligament, and 'pil' is the pubo-ischiadic ligament. Scale bar = 1 cm.

as the attachment for hypaxial musculature (*M. obliquus abdominus*). The ligament is ventral to the PIFI (= *Mm. iliotrochanterici, partim* of Aves) and *N. femoralis*. Thick fascia with similar topological relationships are present in this region in Chelonia and Crocodylia, extending from the ilium to the proximal

pubis (pers. observ.; Romer, 1923a: 534–535). This brings to question what degree of fibrosity of an elongate, membranous, non-contractile structure is required to qualify it as a 'ligament'. Under some definitions of 'ligament', these fascia could qualify as diminutive ilio-pubic ligaments. In the absence of contrary evidence,

I will assume that these fascia are character state variations of the character 'ilio-pubic ligament'.

Polarity of this character is not clear, but fossil outgroup data and the specialized pelvises of Chelonia and Crocodylia allow the inference that the ilio-pubic ligament is secondarily reduced in these two clades. For example, crocodylians have reduced the pubic tubercle and the cranial process of the ilium (Russell & Wu, 1997). The more prominent pubic tubercle and cranial iliac process of non-crocodylian archosauriforms may signal the presence of an ilio-pubic ligament in these taxa. In this case, Lepidosauria (and their fossil outgroups) may offer an approximation of the ancestral reptilian (and archosauromorph) ilio-pubic ligament morphology (Fig. 19C). The ligament would have reduced in Archosauriformes (especially crocodylians) with the pubic tubercle, perhaps as the PIFI origins moved dorsally, but the ilio-pubic ligament remained present on the line to Neornithes.

#### *Pubo-ischiadic ligament*

The homology of the pubo-ischiadic ligament is strongly supported. This ligament (Fig. 19: pil) is well developed in Chelonia and Lepidosauria (Romer, 1922, 1956; Haines, 1935), which apparently have the ancestral reptilian condition. It connects the pubic tubercle (and ilio-pubic ligament) to the ischial tuberosity (and ilio-ischiadic ligament). The pubo-ischiadic ligament lies superficial to all of the ventral thigh muscles, except for parts of the flexor cruris group in non-archosaurs, which originate from the ligament along with the ADD. The pubo-ischiadic ligament (my usage) is a different structure than the connective tissue in extant Reptilia (called the pubo-ischiadic ligament by Parrish, 1991) that is embedded in the abdominal musculature along the midline of the body, between the pubic and ischial symphyses.

My dissections of crocodylians have revealed the presence of a small, flimsy pubo-ischiadic ligament (Fig. 19B: pil). To my knowledge this structure has been illustrated previously (e.g. Gadow, 1882a: fig. 32; cf. fig. 31) but not discussed. It extends from the fascia of *M. obliquus abdominus internus* near the proximal pubis to the ischial tuberosity and caudal muscle fascia (e.g. *M. ischio-caudalis*). The ligamentum ischio-pubicum (Fig. 19A: ipl) is present in Neornithes connecting the obturator tuberosity (see Ischial Structures, p. 153) to the caudolateral surface of the proximal pubic shaft (a small tubercle is sometimes present there, near the preacetabular tubercle).

Based on the presence of a similar ligament in a similar position in all extant Reptilia, and the presence of osteological correlates (the pubic tubercle, ischial tuberosity, and/or obturator tuberosity) in fossil Reptilia, the hypothesis of homology of this pubo-ischiadic

ligament is sustained. This contrasts with previous suggestions (Romer, 1922, 1923b, 1956; Haines, 1935) that the pubo-ischiadic ligament is absent in archosaurs. Like the ilio-pubic ligament, it was merely reduced with the pubic tubercle and ischial tuberosity in Archosauriformes (Fig. 19C: pil). The pubo-ischiadic ligament changed slightly on the lines to Crocodylia (further reduced with the pubic tubercle and the evolution of kinetic pubes) and Neornithes (reduced and shifted its position onto the obturator tuberosity as the pubes were retroverted).

The single ADD muscle originates from the ligament ancestrally in Reptilia (Gadow, 1882a; Romer, 1922, 1923b). In archosaurs, the paired ADD1 + 2 are present on the ischium, so the reduction of the pubo-ischiadic ligament may have coincided with a shift of the adductor origins, and perhaps division of the ADD into two heads (Fig. 16; see Pubo-Ischiadic Plate, pp. 137, 152–153). Neornithes only modified this condition slightly: the second (lateral) adductor origin may have moved cranioventrally to lie closer to the first (medial) origin as the obturator process and PIFE3 were reduced (Fig. 16; see Obturator Process, pp. 152–153).

The flexor cruris muscles of extant archosaurs probably fragmented and reduced as the pubo-ischiadic ligament was modified, which correlates with the disparity between crocodylian and neornithine flexor cruris muscles. The specifics of these changes are difficult to resolve because flexor cruris muscle homologies remain controversial.

If the pubic tubercle diverged into proximal and distal portions, as data from a few archosauriforms intimates (see Pubic Structures, p. 142), the proximal portion remains correlated with the pelvic ligaments, *M. obliquus abdominus*, and the AMB. The distal portion is related to the attachments of *M. rectus abdominus* (Walker, 1977; Tarsitano, 1991) as well as connective tissue running between the distal pubes and ischia (Parrish, 1991).

#### *Ilio-ischiadic ligament*

The ilio-ischiadic ligament (Fig. 19: iil) extends from the ischial tuberosity (and pubo-ischiadic ligament) to the ventral rim of the postacetabular ilium in Squamata. It is the origin of parts of the flexor cruris group and occasionally some parts of other thigh muscles. Only flexor cruris musculature, the fascia of the caudal musculature (e.g. *M. ilio-ischio-caudalis* and *M. transversus perineus*), and the ilio-ischiadic membrane are present in this area in other Reptilia.

Considering data from extant taxa, a distinct ilio-ischiadic ligament might appear to be exclusive to Squamata among extant Reptilia. It may have evolved after the divergence of Squamata and Rhynchocephalia from their common lepidosaurian ancestor (*contra*

Romer, 1922, 1956; Haines, 1935). However, I consider the dense fascia present in this region in other Reptilia to be sufficiently similar to the squamate condition to recognize them as variations of the same character (ilio-ischiadic ligament). Indeed, Chelonia and Crocodylia may have reduced this ligament much like they reduced the ilio-pubic ligament. The ilio-ischiadic membrane of Neornithes could be interpreted as a derived character state of the ilio-ischiadic ligament because its position is topologically similar, its soft tissue connections are similar, and some osteological correlates (see pp. 152–153) are present in fossils.

The soft tissues that are correlated with the ischial tuberosity vary among extant taxa, yet the tuberosity is present in many basal Reptilia despite these differences. One consistent relationship is the connection of the ischial tuberosity to the ilio-ischiadic ligament (or membrane/fascia). Thus I infer that the ischial tuberosity of Archosauriformes retained its ancestral connection to the ilio-ischiadic ligament (Fig. 19C: iil). More data from fossils (e.g. the ischial tuberosity or proximal dorsal process of the ischium) would be useful to further test this hypothesis of transformation.

#### *Summary of membrane and ligament evolution*

The three main pelvic ligaments were reduced in archosauriforms as many muscles shifted their origins (the flexor cruris and ADD), were lost (parts of the flexor cruris, and *M. pubotibialis*; Romer, 1923b, 1942), or fragmented (the flexor cruris and ADD). When the pubes and ischia expanded ventrally within Archosauriformes, a sagittal pubo-ischiadic membrane formed in the fenestra between them. This membrane split into two halves as the pubic and ischiadic symphyses ‘unzipped’ within Theropoda. Within Aves, an ilio-ischiadic membrane (a derivative of the ilio-ischiadic ligament), connected the dorsal ischium to the ventral ilium as an ilio-ischiadic fenestra formed and the origin of the ISF (= ISTR) moved laterally. The pubo-ischiadic membrane became two lateral membranes in *Patagopteryx* + *Ornithurae* as the OM (= PIFE2) shifted onto it. Although many modifications have evolved, Neornithes retains the three main pelvic ligaments that most other Reptilia have.

### SUMMARY

Character optimization (Appendix 3) reconstructs the ancestral archosauromorph as having the following features: an unexpanded ilium with two sacral vertebrae, and a relatively small IF muscle; a complete pubo-ischiadic plate that lacks pronounced pubic or ischiadic aprons (Fig. 7) and has little subdivision within its PIFI (medially) and PIFE (laterally) origins; an AMB originating close to the pubic tubercle (Figs

2, 12); large pubic and ischial tuberosities connected to robust pelvic ligaments (Fig. 19) and their associated flexor cruris and adductor muscles (Fig. 2); and medial origins of the ISTR (ischium; Fig. 2) and the CFB (caudal vertebrae, sacrum, and ilium; Figs 2, 6).

On the line to Neornithes, basal archosauriforms had a slightly expanded preacetabular ilium, indicating some cranial expansion of the IF and part of *M. iliotibialis* (Fig. 8). These taxa also reduced the pelvic ligaments with the pubic and ischial tuberosities (Fig. 19C). The pubic tubercle may have diverged into proximal and distal portions that were connected to different soft tissues (Figs 12–14). An ischial ridge (and scar) signals a modification of the ADD into two muscles originating from the lateral ischium (Fig. 16). The pubes and ischia were elongated into aprons (Figs 8–12), perhaps corresponding to shifts of the origins of the PIFI1+2 (dorsally) and the PIFE1 (onto the cranial pubic apron; Fig. 14). The elongate ventral pelvis enclosed a pubo-ischiadic fenestra, possibly occupied only by a thin medial membrane (Fig. 18). The ancestral archosaur changed little from this condition, and Crocodylia largely retains this plesiomorphic suite of characteristics.

The pubes and ischia elongated further in ancestral Dinosauriformes as the PIFE musculature became more widely separated (Figs 8, 11). Ancestral Dinosauria expanded the sacrum, ilium, and IF cranially, and the brevis fossa indicates a partial lateral shift of the CFB origin (Fig. 6). Theropoda retained this condition ancestrally; the distal ischial tubercle suggests a FTI1 origin (similar to Crocodylia; Fig. 16), but more data are needed from basal taxa to corroborate or refute this. Neotheropoda expanded the sacrum, ilium, and IF even further cranially, and had robust pubic and ischiadic boots correlated with modifications of abdominal muscles (Fig. 11).

Profound changes occurred within Avetheropoda and more basal Tetanurae. The preacetabular (‘cupped-icus’) fossa alludes to some lateral movement of the PIFI origins onto the ilium (Fig. 6), and the ventrally open pelvic canal indicates widely separated pubic (parts 1+2) and ischial (part 3) PIFE origins (Figs 9–14). Enlargement of the pubic boot suggests additional changes in abdominal musculature such as a shift of *M. ischiocaudalis* off the ischium onto the pubic boot. Maniraptoriform ischia had a distinct, proximal obturator process with a small PIFE3 origin, whereas maniraptorans reduced the distal ischium (Fig. 15) and the cranial portion of the pubic boot, signalling additional changes of the abdominal musculature and perhaps the ischial flexor cruris muscles.

Some of the most profound pelvic changes evolved in Eumaniraptora before the origin of flight in Aves. The iliac process supratrochantericus is correlated

with more distinct separation between the preacetabular and postacetabular iliac concavities (Fig. 4). The brevis and preacetabular fossae were reduced as the CFB and PIFI muscles shifted further laterally (Fig. 6). The pubic tubercle became more cranially oriented and crestlike, but associated soft tissues (the ilio-pubic ligament and *M. obliquus abdominus*) probably changed little. The pubes became more retroverted and the aprons were reduced further distally (Figs 8–11), moving the PIFE1+2 origins with them and expanding the lateral portion of the pubo-ischiadic membrane (Fig. 18). The ischial obturator tuberosity signals a repositioning of the pubo-ischiadic ligament that accommodated a shift of the PIFE2 origin (and line of action).

Reduction of the ischial symphysis, retroversion of the ischia, and associated changes in the ilio-ischiadic region are consistent with the inference that an ilio-ischiadic membrane may have evolved from the ilio-ischiadic ligament (Figs 18, 19) as the ISTR origin moved laterally and hypaxial muscles changed. The proximal dorsal process of avialan ischia is a modified ischial tuberosity (Fig. 15) that appears to be correlated with the formation of an ilio-ischiadic membrane. The anatomical significance of the distal dorsal ischial process in Aves is not well understood, but it may also relate to ilio-ischiadic membrane or flexor cruris muscle evolution.

Expansion of the sacrum and corresponding elongation of the ilium occurred within Aves, moving the IF origin cranially. Contact between the distal ischia was eliminated along with the obturator process and presumably the PIFE3; the adductor muscles may have concurrently shifted to their derived neornithine positions (Fig. 16). The brevis fossa disappeared altogether in Pygostylia, so the CFP (=CFB) origin probably was fully lateral. Increased retroversion of the pubes and ischia (Figs 8, 11) moved the PIFM + PIFL (=ADD1+2), FCM (=FTI3), ISF (=ISTR), and OL + OM (=PIFE1+2) relative positions caudally.

Neornithes acquired its last few derived pelvic characteristics within Ornithothoraces, especially Ornithurae. Except for some basal taxa (e.g. Enantiornithes), these birds lost the pubic symphysis, apron, and boot in conjunction with attaining a fully medial OM (=PIFE2) origin and a laterally positioned pubo-ischiadic membrane (Figs 14, 18). Some modifications of hypaxial muscles probably also evolved in these taxa. Only minor changes such as additions of sacral vertebrae occurred between *Patagopteryx* + Ornithurae and Neornithes. The stage was already set for future pelvic specializations long before crown group birds diversified.

## CONCLUSION

This study emphasizes the importance of both palaeontological and neontological data in understanding

musculoskeletal evolution (for similar approaches see Parrish, 1983; Gatesy, 1995; Witmer, 1995, 1997). The major concept that unites these data is homology. My perspective that emphasizes homology in studying character evolution on the line to Neornithes suggests some general closing points:

(1) Palaeontological data are indispensable for studies of soft tissue evolution because fossils have osteological, and hence soft tissue, character states intermediate between those of disparate extant clades. Thus data from fossils assist polarity assessment with soft tissues (Witmer, 1995) as well as assessment of osteological homologies. As Gauthier *et al.* (1988: 193) recognized, “fossils should be most important in phylogenetic inference when the group of interest is old and only a few, highly modified terminal taxa are extant”. This is the case for Archosauria. Romer’s (1923a,b,c, 1927a,b, 1942) thigh muscle homologies were based on anatomical and ontogenetic data solely from extant taxa, and were not phrased in a phylogenetic context emphasizing character congruence. The case for those homologies may strengthen or weaken with the addition of palaeontological data.

As a corollary, using two or more extant ‘bracket taxa’ (e.g. crocodylians and neornithines) to reconstruct the soft tissue anatomy of one extinct taxon can give inaccurate results if these reconstructions do not also consider data from extinct bracket taxa. Information from fossil archosauriforms appears to be more critical than data from basal Reptilia because these fossil data reveal key osteological (and soft tissue) transformations on the lines to Crocodylia and Neornithes. For example, a reconstruction of the thigh musculature of the sauropod *Diplodocus* using only data from Crocodylia, Neornithes, and *Diplodocus* would be flawed in many aspects. Many details of the pelvic soft tissue anatomy of extinct archosaurs remain obscure without vital skeletal data from their extinct relatives. A broad spectrum of fossil and extant outgroups is necessary to infer many details of soft tissue anatomical evolution. My study demonstrates this point many times over: more data yield more resolution.

(2) Of course, neontological data on soft tissue anatomy are necessary for reconstructing soft tissues in extinct taxa (Bryant & Russell, 1992; Witmer, 1995). An outgroup-based phylogenetic perspective is necessary; using single-taxon exemplars for reconstructing dinosaur soft tissue anatomy (e.g. Romer, 1923c; Tarsitano, 1983) is an unsafe practice (also see Gatesy, 1995). In addition, soft tissue data (whether direct or inferential) add more biological (e.g. functional, or anatomical) relevance to systematic characters (Witmer, 1995). Many osteological correlates that I have noted in this study were used by other authors as systematic characters, sometimes without comment on their possible anatomical or functional significance

(e.g. soft tissue relationships). Neontological data from structure-function studies in living animals are also important for understanding the functions of homologous and analogous structures in extinct taxa (Gatesy, 1995). Ignoring palaeontological or neontological data in studies of the evolution of morphology or function can lead to erroneous conclusions.

(3) One problem for studies of archosauromorph pelvic evolution is that some homologies of skeletal morphology have not been explicitly addressed, or are erroneous. This problem has led to some confusion and errors in nomenclature, soft tissue reconstructions, functional interpretations, comparisons among taxa, evolutionary inferences, and scenarios of locomotor and physiological evolution. I emphasize that homology not only of osteological structures, but also of bone surfaces, should be explicitly addressed. This is particularly important for reconstructing soft tissues in extinct forms, as my examples from the pubo-ischiadic plate as well as the PIFE and PIFI musculature illustrate.

(4) Many details that I have reconstructed would not be revealed by a more narrow or a poorly sampled analysis. I have advocated 'lumping' many characters that were previously coded as independent into separate states of a single character. Many problems arise when essentialism is overemphasized in character analyses and the test of similarity is too strictly applied. Seemingly dissimilar osteological features such as pits, scars, tubercles, and processes often occur as separate states of the same character and blur together as ontogenetic and phylogenetic continua. Their associated soft tissues, especially if consistent in relative position among extant taxa, help resolve the polarity of osteological character states.

For example, if a muscle or ligament that ancestrally attaches to a small rugosity on a bone is present on a large bony process in a derived state, it is inferred as having shifted its position as this process evolved from the rugosity. The rugosity and the process might be coded as separate characters rather than states of the same character if their soft tissue correspondence is not recognized. This would be a case where the test of similarity in homology assessment was too rigidly applied, emphasizing taxic homology (lack of change or variation) over transformational homology (presence of change or variation). This is precisely the case for the ischial tuberosity and proximal dorsal ischial process: they have been seen as unrelated features (e.g. Holtz, in press).

The sundry structures of the pubes and ischia of archosauromorphs provide many examples of how some 'different' structures may be usefully seen as parts of character state continua rather than discrete steps. In the Appendices, I partition such characters into multiple character states, many of which are

clearly steps along a continuum and not entirely discrete. I optimize some of these characters as ordered (Maddison & Maddison, 1992) for this reason. I recognize that there are alternative ways to code characters, such as breaking multistate characters into multiple binary 'presence/absence' characters (Pleijel, 1995; Wilkinson, 1995). Because my goal in this study is to elucidate potential homologies and transformations within complex anatomical systems, I prefer the approach of 'lumping' several potential binary characters into single multistate characters when I feel that the evidence for such a complex transformation series is strong. In either case, it is a matter of personal judgement that should be explicitly justified.

(5) Many osteological (and soft tissue) features of the neornithine pelvis are commonly considered 'avian'. Yet many of these features are synapomorphies for clades that are more inclusive than Aves or Neornithes. For example, on the line to Neornithes, roughly seven character states changed in non-archosaurian Archosauromorpha, 45 states changed in non-avian Ornithodira, and 18 states changed within Aves, totalling about 70 changes on the archosaurian line to Neornithes (see Appendix 3). In contrast, roughly 17 character states changed on the archosaurian line to Crocodylia. As has long been recognized, crocodylian pelvises retain more plesiomorphies than neornithine pelvises.

In my analysis, only five derived pelvic character states (two are equivocal) separate birds (Aves) from non-birds, in contrast to nine derived states (three are equivocal) separating Eumaniraptora from other maniraptorans. Only one character state optimizes as unique to Neornithes: 11 or more sacral vertebrae. All other character states listed in Appendix 3 are plesiomorphic for Neornithes, or were intermediate states preceding modern derived states. Some traits (e.g. the brevis and preacetabular fossae, pubic and ischiadic aprons and boots, and some ischial structures) are unique to extinct taxa. However, they are optimized as present on the line to Neornithes, and thus are relevant for understanding the anatomical and functional changes that preceded the origin of Neornithes.

No single node on the line to Neornithes holds the trump card for 'bird-like' status. What seems morphologically 'bird-like' or 'avian' from a neontological or neornithine point of view actually evolved in a protracted, stepwise pattern on the archosauromorph line to Neornithes. Basal Ornithodira, Theropoda, and Maniraptora lack some derived pelvic characteristics of Neornithes, but likewise so do basal Aves, Pygostylia, and Ornithothoraces. Intermediate character states are present along this line to extant birds, revealing the evolutionary sequence of assembly and modification by which Neornithes acquired its derived character states. Some

homologies of characters and character states remain unresolved or very tentative, pending the discovery and description of fossils that clarify character optimization. However, I have resolved many homologies that have not been explicitly addressed by previous authors, and I have established the sequence of many anatomical transitions along the line to Neornithes.

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## APPENDIX 1

Characters and character states that were optimized on the 'consensus' phylogenetic framework (Fig. 3) to trace character evolution (see Material and Methods). Characters marked with an asterisk (\*) may be character states of a previously listed character; see the text for details. Ordered characters are noted.

(1) Number of sacral vertebrae: two (0), three or four (1), five (2), six (3), seven (4), eight or nine (5), ten (6), or eleven or more (7). Ordered.

(2) Cranial iliac process (Figs 4, 8: cp): small or absent (0), present but not well expanded (brachyliac; 1), or present and well expanded (dolichoiliac; 2). Ordered.

(3) Processus supratrochantericus (Table 3A): absent (0) or present (1).

\* (4) Vertical iliac ridge (Table 3A): absent (0) or present (1).

(5) Brevis fossa (Table 3): absent (0), present and large (1), or present but reduced (2).

(6) Preacetabular fossa (Table 3): absent (0), present and large (1), present but reduced onto lateral ilium (2), or present but strongly reduced (3).

(7) Ischial ridge and scar for the ADD2 (Figs 8, 16: ir): absent (0) or present (1).

(8) Pubic symphysis: unexpanded (0), expanded as apron (1; Figs 9, 10, 12: pa), apron reduced (2), or absent (3).

(9) Ischiadic symphysis: unexpanded (0), expanded as apron (1; Figs 9, 10: ia), apron reduced (2), or absent (3).

(10) Pubes and ischia (Figs 8, 11): short (0), distal ends elongated (1), or very elongate (2). Ordered.

(11) Ventral floor of the pelvic canal: closed or barely open (0) or widely open as a pelvic fenestra (1; Fig. 9: pef).

(12) Pubic foramen in the distal pubic apron (Figs 9, 10: pf): absent (0) or present (1).

(13) Secondary 'thyroid' foramen in the proximal pubis (Fig. 8: sf): absent (0) or present (1).

(14) Obturator foramen in the proximal pubis (Figs 8, 9: of): present (0) or absent (1; foramen opens into obturator notch [on]).

(15) Obturator process on the ischium (Figs 8, 11, 15: op): not distinct from the rest of the pubo-ischiadic plate (0), proximal and conspicuous (1), distal and reduced (2), very distal and reduced (3), or absent (4).

- (16) Pubic tubercle (Table 4): large and elongate (0), reduced to a rugosity (1), or spine or crestlike, and pointing cranially (2).
- (17) Pubic retroversion (Figs 8, 11): pubis cranially oriented (0), pubis at or slightly behind vertical (1), or pubis well retroverted (2). Ordered.
- (18) Pubic boot (Figs 10, 11, 13: pb): absent (0), knoblike (1), present as a craniocaudal expansion (2), or reduced to only a caudal boot (3).
- (19) Ischial tuberosity (Table 5A): large and elongate (0), reduced to a rugosity (1), or expanded into a proximal dorsal ischial process (2).
- (20) Distal ischial tubercle (Table 5B): absent (0) or present (1).
- \*(21) Distal dorsal ischial process (Table 5B): absent (0) or present (1).
- (22) Obturator tuberosity on the ischium (Table 5C): absent (0) or present (1).
- (23) Ischial boot (Figs 9–11: ib): absent (0) or present (1).
- (24) Length of the ischium relative to the pubis (Figs 8, 11): subequal (0) or much shorter (1).

APPENDIX 2

24-character data matrix showing scored character state values among the 45 saurian taxa used in this study. Ancestral states are denoted as (0), derived as (1) through (7), and missing or equivocal data as (?).

	1		11111		11112		2222	
	12345	67890	12345	67890	1234			
Lepidosauromorpha	00000	00000	00000	00000	0000			
Rhynchosauria	00000	00000	00000	00000	0000			
<i>Trilophosaurus</i>	00000	00000	00000	00000	0000			
Proterosuchidae	00000	01000	00000	10010	0000			
Erythrosuchidae	01000	01111	00000	10010	0000			
<i>Doswellia</i>	11000	01000	00000	10010	0000			
<i>Euparkeria</i>	01000	0?112	00100	10010	0000			
Proterochampsidae	01001	01000	10000	10010	0000			
Ornithosuchidae	1100?	01112	00100	10010	0000			
Parasuchia	01000	01111	00000	10010	0000			
Aetosauria	01000	01111	00100	10010	0000			
Rauisuchidae	01000	01112	1?000	10110	0010			
	1	1						
Poposauridae	11000	01112	11000	10210	0010			
'basal Crocodylomorpha'	01000	01112	10000	10110	0000			
'basal Crocodyliformes'	01000	01222	100?0	10010	0000			
Crocodylia	00000	01221	1001?	?0010	0000			
Pterosauromorpha	11000	0?000	00000	?00?0	0000			
<i>Lagerpeton</i>	01000	01111	00000	10010	0000			
<i>Lagosuchus</i>	01000	01112	10000	100?0	0000			
<i>Lewisuchus</i>	?1?00	0?1?2	?000?	1001?	????			
Ornithischia	21001	01222	10001	220?0	0000			
			2					
Sauropodomorpha	11001	01112	00000	10010	0010			

<i>Eoraptor</i>	1100?	0?1?2	0000?	100??	0?00			
Herrerasauridae	01000	01112	00000	11211	0000			
Coelophysoidea	22001	01112	01100	10110	0010			
Ceratosauria	32001	01112	01000	1011?	0010			
	4							
'basal Tetanurae 1'	22001	01112	01000	10111	0010			
'basal Tetanurae 2'	22011	01112	01000	10211	0010			
				1				
Carnosauria	22001	11112	110?1	10211	0010			
'Basal Coelurosauria'	220?1	11112	110?1	1021?	0010			
Tyrannosauridae	22011	11112	11011	20220	0000			
Ornithomimosauria	22011	11112	11011	10210	0010			
Oviraptorosauria	32002	?1112	11012	102?0	0001			
Therizinosauroidae	22011	11122	1?012	?13?1	00?0			
Troodontidae	32?02	11222	11012	213?0	0101			
Deinonychosauria	22102	21222	11012	2132?	?101			
Alvarezsauridae	22001	0?232	1?014	210?0	0?00			
		3		23				
<i>Archaeopteryx</i>	22102	2?232	1?013	21320	1?01			
<i>Rahonavis</i>	32102	2?232	11013	21320	1?01			
<i>Unenlagia</i>	42102	2?232	11012	?132?	??01			
Confuciusornithidae	42100	21232	1?014	22120	1?01			
Enantiornithes	52100	21232	1?014	22320	1101			
<i>Patagopteryx</i>	52101	01332	1?014	?2020	?100			
Hesperornithiformes	62100	01332	1?014	22000	0000			
	7							
Ichthyornithiformes	62100	0?332	1?014	220?0	?100			
Paleognathae	72100	01332	1?014	220?0	0100			
Neognathae	72100	01332	1?014	220?0	1100			

APPENDIX 3

Node-by-node list of character state optimizations along the line to Neornithes, using the data from Appendices 1 + 2 on the phylogenetic framework from Figure 3 (in MacClade 3.08). Because the phylogenetic framework has several polytomies I used the 'hard polytomy' option (under Trees: Polytomy Options). For purposes of brevity, I prefer this option rather than checking all possible resolutions of polytomies. More equivocality arises if the polytomies are treated as soft. Tree length is 131 steps, consistency index 0.35, retention index 0.78.

The character state changes listed in the Discussion (closing point #5) were reconstructed using the Trace All Changes function in MacClade. Almost all possible changes (approximate maximum amount of changes) were optimized. See Maddison & Maddison (1992) for more information.

Format is: character number (state number). '\*' indicates that the character state optimization is equivocal below that node, and hence the change may have occurred earlier on the line to Neornithes. These characters were mapped using the 'Trace Character' option in MacClade 3.08.

- Archosauriformes: 7(1), 16(1), 19(1).
- Archosauriformes (except Proterosuchidae): 2(1).
- Archosauria: 8(1)\*, 9(1)\*, 10(1)\*.
- Dinosauriformes: 10(2).
- Dinosauria: 1(1)\*, 5(1).

Neotheropoda + Herrerasauridae: 20(1)\*.  
Neotheropoda: 1(2), 2(2), 12(1), 18(1)\*, 23(1).  
Avetheropoda (some of these changes occurred in more basal Tetanurae): 6(1), 11(1), 15(1)\*, 18(2).  
Maniraptoriformes: 14(1), 20(0)\*.  
Maniraptora: 15(2), 23(0)\*.  
Eumaniraptora: 5(2), 6(2), 8(2), 15(3), 16(2), 17(1)\*, 18(3)\*, 22(1), 24(1)\*.

Aves: 1(3), 3(1)\*, 9(3)\*, 19(2), 21(1).  
Pygostylia: 1(4), 5(0), 15(4), 17(2).  
Ornithothoraces: 1(5).  
*Patagopteryx* + Ornithurae: 6(0), 8(3), 18(0), 24(0).  
Ornithurae: 1(6).  
Neornithes: 1(7).