EVOLUTION OF THE PECTORAL GIRDLE AND FORELIMB IN SAUROPODOMORPHA (DINOSAURIA, SAURISCHIA): OSTEOLOGY, MYOLOGY AND FUNCTION

von

Dipl.-Geol. Kristian Remes

Dissertation der Fakultät für Geowissenschaften

der Ludwig-Maximilians-Universität München

zur Erlangung des Doktorgrades (Dr. rer. nat.)

Eingereicht zur Beurteilung am 06.12.2007

Betreuer: PD Dr. Oliver Rauhut,
Ludwig-Maximilians-Universität München

Zweitgutachter: Prof. Dr. Martin Sander,
Rheinische Friedrich-Wilhelms-Universität
Bonn

Datum der mündlichen Prüfung: 21.04.2008

温子、真摯な支えとその愛に。

0 Contents

Anatomical abbreviations

Osteology

ac	accessory distal condyles on humerus
acr	acromion
adp	apex of deltopectoral crest
ar	acromial ridge
ambb	attachment of M. biceps brachii
ameu	attachment of M. entepicondylo-ulnaris
amhr	attachment of M. humeroradialis
amsc	attachment of M. supracoracoideus
amtb	attachment of M. triceps brachii
amtbc	attachment of coracoidal anchor of M. triceps brachii caput coracoscapulare
bt	biceps tubercle on coracoid
ccl	contact for clavicle
cdp	caudodistal process on scapula
cdr	distal condyle of radius
cdu	distal condyle of ulna
ce	centrale
cf	caudal flange on scapular blade
chr	humeral cotyle of radius
chu	humeral cotyle of ulna
cid	caudal intercondylar depression
cl	clavicle
cne	centrale
co	coracoid
cocp	caudal process of coracoid
cof	coracoid foramen
cp	cranial process of ulna
cpt	caudoproximal tubercle of radius
crdt	craniodistal tubercle of radius
crp	craniodistal process on scapula
crr	cranial ridge on radius
dc	distal carpal(s)
dcr	dorsocranial ridge on humerus
de	distal expansion of scapula
did	dorsal intercondylar depression
dp	deltopectoral crest
drc	distal radial condyle
ep	extensor pit(s)
et	extensor tubercle(s)
fc	caudal facet on ulna
fcm	craniomedial fossa of coracoid
fmc	facet for M. cucullaris
fmcb	fossa for M. coracobrachialis (brevis)
fmdc	facet for M. deltoideus clavicularis
fmds	fossa for M. deltoideus scapularis
fmeu	facet for M. ectepicondylo-ulnaris
fmfdl	facet for origin of M. flexor digitorum longus
fmfdp	fossa for M. flexor digitorum profundus
fmpq	fossa for M. pronator quadratus
fmsc	fossa for M. supracoracoideus (pars scapularis)
fmscs	fossa for M. subcoracoideus
fmsh	fossa(e) for M. scapulohumeralis
fmsm	facet for M. supinator manus
fmsp	facet for M. serratus profundus
fmss	facet for M. serratus superficialis
fmssc	facet for M. subscapularis
fmtbh	facet(s) for M. triceps brachii capiti humerales mediales
fmtbhm	facet for M. triceps brachii caput humerale mediale
fr	radial fossa on ulna
ft	flexor tubercle
fvm	ventromedial fossa of coracoid
gl	glenoid cavity
h	humerus
hh	humeral head
hlt	lateral tubercle of humerus
hmt	medial tuberosity of humerus
hrc	radial condyle of humerus
huc	ulnar condyle of humerus
i	intermedium
icb	impressio m. coracobrachialis
icl	interclavicle
imr	intermuscular ridge(s)
lepc	ectepicondyle
lfmc	lateral flange(s) of metacarpal(s)
lp	lateral process of ulna
m	manus
mc	metacarpal
mcdc	metacarpal distal condyles
mcep	metacarpal extensor pit(s)
mclp	metacarpal ligament pit(s)
mepc	entepicondyle
ol	olecranon process

pcs	processus sternocoracoidei
ph	phalanx, phalanges
plp	phalangeal ligament pit(s)
pi	pisiform
pua	proximal ulnar articular facet of radius
r	radius
rae	radiale
rcp	radial caudoproximal process
rcr	radial cotyle of radiale
rct	radial cranioproximal tubercle
rnsc	recessus for N. supracoracoideus
rt	radial tubercle (= tmb?)
rup	radial ulnar process
sa	sternocoracoidal articulation
sc	scapula
sca	scapulocoracoidal articulation
scb	scapular blade
sch	scapular head
scs	scapulocoracoidal suture
sgb	supraglenoidal buttress
sgf	subglenoidal fossa on coracoid
smld	scar for M. latissimus dorsi
ssc	suprascapula
ssca	suprascapular articulation
ste	sternum
stp	sternal plate
tmb	tubercle for M. brachialis
tmbb	tubercle for M. biceps brachii
tmtbs	tubercle for M. triceps brachii caput scapulare
ua	ulnar articular facet on radius
ucu	ulnar cotyle of ulnare
ul	ulna
ule	ulnare
un	ungual(s)
urt	ulnar radial tubercle
vip	ventral intercondylar pit

Myology

AD5	M. abductor digiti V
AdA	M. adductor alulae
ADM	M. abductor digiti majoris
AP	M. abductor pollicis
AR	M. abductor radialis
B	M. brachialis
BB	M. biceps brachii
C	M. cucullaris
CB	M. coracobrachialis
CBbrev	M. coracobrachialis brevis
CBcran	M. coracobrachialis cranialis
CBlong	M. coracobrachialis longus
CC	M. costocoracoideus
CCprof	M. costocoracoideus profundus
CCsup	M. costocoracoideus superficialis
DC	M. deltoideus clavicularis
Dmaj	M. deltoideus major
Dmin	M. deltoideus minor
DS	M. deltoideus scapularis
EBA	M. extensor brevis alulae
ECR	M. extensor carpi radialis
EctU	M. ectepicondylo-ulnaris
ECU	M. extensor carpi ulnaris
EDC	M. extensor digitorum communis
EDP	Mm. extensores digitorum profundi
EDS	Mm. extensores digitorum superficiales
ELA	M. extensor longus alulae
ELDM	M. extensor longus digiti majoris
ELDMdist	M. extensor longus digiti majoris pars distalis
EM1	M. extensor metacarpi I
EM4	M. extensor metacarpi IV
EntU	M. entepicondylo-ulnaris
FCR	M. flexor carpi radialis
FCU	M. flexor carpi ulnaris
FDL	M. flexor digitorum longus
FDL1	M. flexor digitorum superficialis
FDL2	M. flexor digitorum profundus
FDM	M. flexor digiti minimi
FDP	Mm. flexores digitorum profundi
FDS	Mm. flexores digitorum superficiales
FDSprof	M. flexor digitorum superficialis pars profundus
FD5	M. flexor digiti V
FPB	M. flexor pollicis brevis
HR	M. humeroradialis
I	Mm. interossei
Idors	Mm. interossei dorsales
Ivent	Mm. interossei ventrales
ID	avian M. interosseus dorsalis
IV	avian M. interosseus ventralis
L	Mm. lumbricales
LD	M. latissimus dorsi
LDcaud	M. latissimus dorsi caudalis
LDcran	M. latissimus dorsi cranialis
LS	M. levator scapulae
LSHL	Lig. scapulohumerale laterale
LSSI	Lig. Sternoscapulare internum
P	M. pectoralis
PA	palmar aponeurosis
PQ	M. pronator quadratus
PT	M. pronator teres
PT1	M. pronator superficialis
PT2	M. pronator profundus
R	M. rhomboideus
S	M. supinator
SC	M. supracoracoideus
SCcor	M. supracoracoideus pars coracoideus
SCscap	M. supracoracoideus pars scapularis
SCS	M. subcoracoscapularis
SCS1	M. subscapularis
SCS2	M. subcoracoideus
SCS3	M. coracobrachialis caudalis
SH	Mm. scapulohumerales
SHcaud	M. scapulohumeralis caudalis
SHcran	M. scapulohumeralis cranialis
SM	M. supinator manus
SP	M. serratus profundus
SS	M. serratus superficialis
StC	M. sternocoracoideus
TB	M. triceps brachii (inserting tendon)
TBC	M. triceps brachii caput coracoideum (*Euparkeria*)
TBCs	M. triceps brachii caput coracoscapulare
TBHlat	M. triceps brachii caput humerale laterale
TBHmed	M. triceps brachii caput humerale mediale
TBHposticum	M. triceps brachii caput humerale posticum
TBS	M. triceps brachii caput scapulare
TL	transversal ligament
TM	M. teres major
UMD	M. ulnometacarpalis dorsalis
UMV	M. ulnometacarpalis ventralis

Institutional abbreviations

AMNH	American Museum of Natural History, New York, USA
BMNH	The Natural History Museum, London, United Kingdom
BP	Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa
BSC	B. M. Birla Science Centre, Hyderabad, India
CM	Carnegie Museum of Natural History, Pittsburgh, USA
CUT	Geological Museum, Chengdu University of Technology, Chengdu, People's Republic of China
FFCLRP	Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, São Paulo, Brazil
GPIT	Geologisches und Paläontologisches Institut der Universität Tübingen, Tübingen, Germany
GSI-SR	Geological Survey of India, Southern Region, Bandalaguda, Hyderabad, India
ISI	Indian Statistical Institute, Geology Museum, Kolkata, India
IVPP	Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, People's Republic of China
MACN	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina
MB	Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany
MCN	Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil
MCP	Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MLP	Museo de La Plata, University of La Plata, La Plata, Argentina

MN	Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil
MNHN	Muséum National d'Histoire Naturelle, Institute de Paleontologie, Paris, France
NM	Nasionale Museum Bloemfontein, Bloemfontein, South Africa
NMZ	National Museum of Zimbabwe, Bulawayo, Zimbabwe
OUMNH	Oxford University Museum of Natural History, Oxford, United Kingdom
PVL	Instituto de Paleontología, Fundación Miguel Lillo, San Miguel de Tucuman, Argentina
PVLR	Museo de Ciencias Naturales, Universidad Nacional de La Rioja, La Rioja, La Rioja, Argentina
PVSJ	Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, San Juan, Argentina
SAM	Iziko South African Museum, Capetown, South Africa
SMNS	Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
UCMP	University of California Museum of Paleontology, Berkeley, California, USA
UFSM	Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul, Brazil
USNM	United States National Museum, Smithsonian Institution, Washington D.C., USA
YPM	Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA
ZDM	Zigong Dinosaur Museum, Dashanpu, Zigong, Sichuan, People`s Republic of China

1 Introduction

For the general public, sauropods represent one of to the most familiar groups of dinosaurs. They are easy to distinguish from other dinosaurs by their exceptionally long necks and tails, their quadrupedal stance with long, columnar limbs, and particularly by their gigantic dimensions. The mass of the most gigantic sauropods surpasses that of even the largest ornithopods, theropods, and extinct mammals by an order of magnitude: *Argentinosaurus*, the largest well-described taxon, is estimated to have weighed about 78 metric tonnes (Mazzetta et al., 2004). The average sauropod seems to have had a mass well above 10 tonnes, combined with lengths in the range of 10 to 30 meters. Only recently, findings of dwarf sauropods (Sander et al., 2006) or of sauropods with deviant body plan (Rauhut et al., 2005) leave the impression that the spectrum of evolutionary adaptations explored by sauropods was much wider than previously thought.

However, even the stereotype sauropod is a fascinating object of study for many scholars, as exemplified by the wealth of scientific contributions dealing with biomechanics (e.g., Alexander, 1985, 1989; Christian and Preuschoft, 1996; Christian and Heinrich, 1998; Christian et al., 1999a,b; Stevens and Parrish, 1999, 2005a,b; Christian, 2002; Christian and Dzemski, 2007), physiology (e.g., Hohnke, 1973; Weaver, 1983; Daniels and Pratt, 1992; Paul, 1998; Perry and Reuter, 1999; Seymour and Lillywhite, 2000; Burness et al., 2001; Wedel, 2003, 2005), nutrition (e.g., Christiansen 1999, 2000; Upchurch and Barrett, 2000; Barrett and Upchurch, 2005, 2007), growth (e.g., Curry, 1999; Sander, 1999, 2000; Sander et al., 2004; Curry Rogers and Erickson, 2005; Sander and Klein, 2005), reproduction (e.g., Janis and Carrano, 1992; Chiappe et al., 2005) and evolutionary history (e.g., Upchurch, 1995, 1998; Wilson and Sereno, 1998; Wilson, 2002; Upchurch et al., 2004) of these enormous creatures. After the North American ‘bone wars’ between E. D. Cope and O. C. Marsh in the late 19th century (see Colbert, 1997) and the famous sauropod discoveries in Africa and China early in the 20th century (see Lavas, 1997; Sues, 1997; Maier, 2003), academic interest in this group seemed to have diminished for a while, but since the mid 1990s, the number of publications on sauropods has almost doubled to well over 10 per year. Just since the beginning of this project early in 2004, the number of valid sauropod genera increased by almost 40%, from about 90 to 126 in late 2007. The impression comes to one’s mind that we are currently experiencing a ‘gold rush’ of sauropod palaeontology.

The question of sauropod gigantism and limb evolution

Despite this renewed interest in sauropods, much of their biology and evolutionary history is still poorly understood. Especially the most prominent feature of the sauropods, their exceptional gigantism, has remained enigmatic. What specific adaptations enabled these animals to achieve their enormous dimensions? What role played the physical and ecological parameters of their surroundings, such as the Mesozoic atmosphere and flora? And how did these creatures function as giants – how did they stand, walk, breathe, and circulate their blood? How high were their metabolic rates, and how much foliage did they have to consume to meet their demands? These questions formed the starting point of the DFG-funded interdisciplinary Research Unit 533 'Biology of the Sauropod Dinosaurs', initiated and coordinated by Martin Sander of the University of Bonn, and during the first 3-year funding period incorporating 30 German, Austrian, Swiss, and British researchers in 12 subprojects.

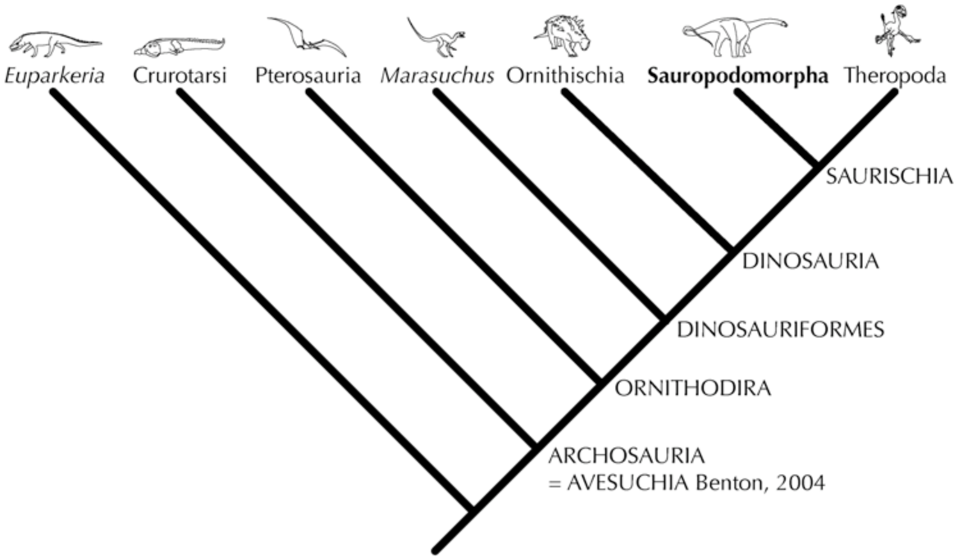

Figure 1-1. Cladogram of the major archosaur groups. The clade Dinosauromorpha, which includes *Lagerpeton* + Dinosauriformes, is not shown (*Lagerpeton* has no forelimb material preserved). Phylogenetic relationships are simplified after Benton (2004).

Among the questions raised above, a crucial aspect for any attempt to interpret and explain sauropod gigantism is the evolutionary history of the group. According to the current paradigm of dinosaur paleontology, all dinosaurs form a monophyletic group and are plesiomorphically bipedal (Sereno, 1991, 1997, 1999; Novas, 1996; Padian, 1997a; Carrano, 1999; Benton, 2004). The ancestral dinosaur is assumed to be a small bipedal runner (below 2 meters long), with short arms and grasping hands, and a carnivorous diet (Sereno, 1997). Moreover, there is a consensus that Dinosauria splits into two monophyletic groups, Ornithischia and Saurischia, the latter comprising the carnivorous Theropoda and the herbivorous Sauropodomorpha (fig. 1-1; Gauthier, 1986; Brinkman and Sues, 1987; Benton, 1990, 2004; Novas, 1992, 1996; Sereno, 1997, 1999; Langer and Benton, 2006). The sauropodomorphs include Sauropoda and 'Prosauropoda', small to medium sized animals with bipedal and quadrupedal forms among them (fig. 1-2; see Galton and Upchurch, 2004, and Upchurch et al., 2004, for reviews). The sauropod ancestor may be among 'prosauropods', if these animals form a paraphyletic group, or both groups share a common ancestor, if prosauropods are monophyletic (see below). Regardless of the interrelationships of sauropodomorphs, it has never been shown in detail how the transition from small, bipedal forms to gigantic, graviportal quadrupeds may have occurred. The appendicular skeleton and musculature are of special interest for this issue, since these organ complexes had to carry and move the enormous masses in living sauropods, and are therefore essential for the understanding of their gigantism.

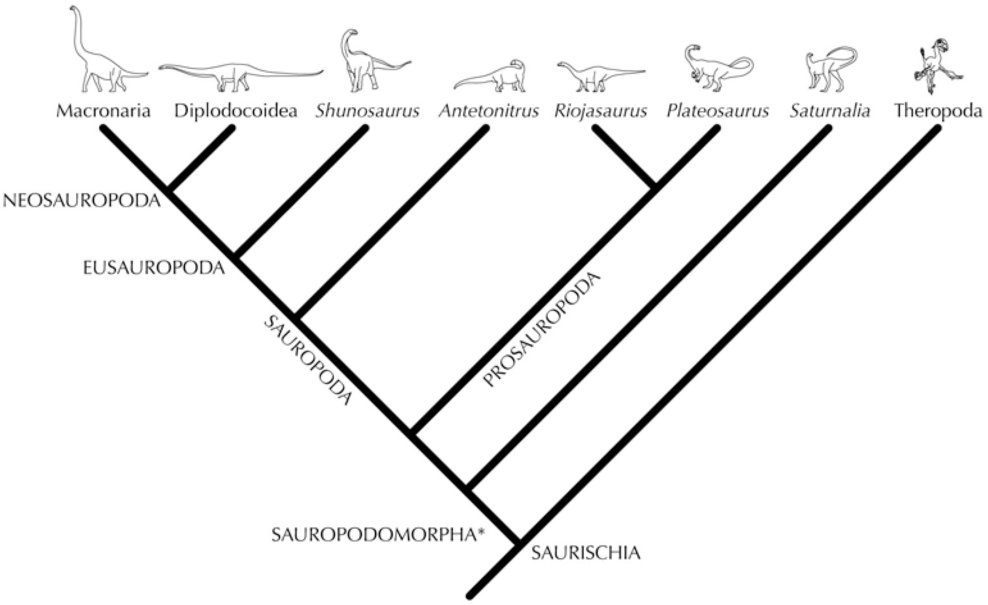

Figure 1-2. Sauropodomorph interrelationships. Simplified cladogram based on Wilson (2002) and Yates (2004). *Note that Sauropodomorpha, Sauropoda, and Prosauropoda form a node-stem-triplet according to the definition of Sereno (1998). Therefore, *Saturnalia* would be excluded from Sauropodomorpha. However, Sauropodomorpha has originally been defined as the stem-based sister taxon to Theropoda (Gauthier, 1986), a definition adopted by most recent works (e.g., Galton and Upchurch, 2004; Yates, 2007).

Both fore- and hindlimbs are highly complex organ systems consisting of a high number of subsystems related to locomotion and support, such as bones, cartilage, joints, ligaments, tendons and muscles. Because of the contrasting morphology of the pectoral and pelvic girdles, their different connection to the axial skeleton, and the strong regional specialization in the bodies of higher amniotes, there is little serial homology among the muscles of the fore- and hindlimb – both systems are independent organs with strongly differing morphology. Therefore, it is to be expected that fore- and hindlimbs underwent completely different modifications during the evolutionary history of the sauropods.

Previous works

Basal sauropodomorphs ('prosauropods') represent one of the least understood groups of dinosaurs, both in respect to phylogenetics and biology. Leal et al. (2004) went so far as to claim "Working with the so-called 'Prosauropoda' is quite frustrating". Early classifications of dinosaurs interpreted these animals as a subgroup of the bipedal, carnivorous theropods (Marsh, 1884b; Lull, 1953), or as ancestors of both carnosaurs and sauropods (von Huene, 1908, 1909, 1914a, 1929, 1932), until Colbert (1964) and Charig et al. (1965) recognized that the group Saurischia consists of two distinct lines, the Theropoda and Sauropodomorpha (Colbert's 'Palaeopoda' + Sauropoda). The latter authors also were the first to emphasize that the hands and feet of prosauropods were not adapted to bipedality as in theropods. They rejected the idea of secondary quadrupedalism in sauropodomorphs as proposed by von Huene (1929, 1932) and assumed that some fully bipedal prosauropods were specialized forms not directly ancestral to sauropods. Galton (1971a) modified this view and regarded prosauropods as facultative bipeds that generally retained the ability to move on all fours at low speeds, probably their usual behavior (Galton, 1973, 1976). His argument is mainly based on the ratio between hind limb and dorsal vertebral column, which is intermediate between typical quadrupeds and unambiguous bipeds in prosauropods. Cluver (1978) and van Heerden (1979) went beyond Galton and suggested that forms like *Plateosaurus* and *Massospondylus* had only semi-erect limbs and were obligate quadrupeds. A view contrasting that of Galton and van Heerden was proposed by Coombs (1978a), who regarded prosauropods as generally bipedal animals, albeit the slowest of all dinosaurian bipeds. Cooper (1981) went even further and reconstructed *Massospondylus* as fully bipedal, endothermic and probably with isolating integument (down feathers). The common interpretation of 'prosauropod' hands as grasping organs (e.g., von Huene, 1905, 1926; Lull, 1953; Galton, 1984b, 1990; Galton and Upchurch, 2004) has supported this view of obligate bipedal 'prosauropods'. However, in his paper on speeds and gaits in various dinosaurs, Thulborn (1982) assumed the larger prosauropods to be fully quadrupedal. The debate on body posture continued during the 1980s, when Galton (1985a) for the first time recognized prosauropods as herbivorous animals. He furthermore proposed that they represent the first high-browsers in tetrapod evolution, able to reach the higher parts of plants by standing upright with support by the tail in a tripodal stance.

At the same time as the posture debate, Cruickshank (1975) and van Heerden (1978) raised the idea that all prosauropods may belong to a specialized group not directly ancestral to sauropods, based on general anatomical dissimilarities. Bonaparte and Vince (1979) and Bonaparte (1986a,b) rejected this hypothesis, stressing that the similarities between both groups weigh far more than the proposed dissimilarities. However, Sereno (1989) revived the idea of Cruickshank and van Heerden, based on the first cladistic analysis of sauropodomorphs. This work opened a long debate on the interrelationships of basal sauropodomorphs, with several workers claiming that prosauropods are a paraphyletic (or even polyphyletic) assemblage that includes the ancestor of the sauropods (Benton, 1990; Dodson, 1990; McIntosh, 1990a,b, 1997; van Heerden, 1997; Padian, 1997b; Bonaparte, 1999; Luo et al., 1999; Luo and Wang, 2000, Yadagiri, 2001; Yates, 2001, 2003a, 2004, 2007; Yates and Kitching, 2003; Reisz et al., 2005), while others supported the idea of a monophyletic Prosauropoda (Galton, 1990; Gauffre, 1995, 1996; Sereno, 1997, 1999a; Upchurch, 1997a,b; Wilson and Sereno, 1998; Benton et al., 2000; Buffetaut et al., 2000; Hinic, 2002; Martínez, 2002; Pisani et al., 2002; Galton and Upchurch, 2004). In this context, it has been put forward by some authors that the anatomy of the grasping hand of prosauropods was too specialized to be ancestral to sauropods (Sereno, 1989, 1997; Galton, 1990; Christiansen, 1997; Wilson and Sereno, 1998; Martínez, 2002). The analyses of Yates (2003a, 2004), Yates and Kitching (2003), and Upchurch et al. (2007) in a way provide a compromise between both standpoints, resolving a monophyletic core of prosauropods (Prosauropoda *sensu strictu*), while other taxa traditionally placed in Prosauropoda are either stem-sauropodomorphs or still prosauropod-like members of a stem-based Sauropoda (fig. 1-2). The debate on sauropodomorph interrelationships continues, since in the most recent analysis ‘Prosauropoda’ completely dissolves into a paraphyletic set of successive sister taxa to Sauropoda (Yates, 2007).

In comparison, modern scholars studying higher sauropodomorphs (i.e., sauropods) are closer to consensus with regard to locomotor functional morphology and phylogenetic relationships. Soon after the recognition of the Sauropoda as a distinct group of dinosaurs (Marsh, 1878) a general consensus emerged that sauropods were semi-aquatic animals (Cope, 1878a,b; Marsh, 1883, 1884a), mainly based on their cranial and cervical anatomy, although earlier accounts already have interpreted the limbs of these animals as those of fully terrestrial creatures (Marsh 1877a,b; Cope 1878c,d). Dollo (1906) put forward that sauropods are primary quadrupeds, a view generally accepted until the paradigm of plesiomorphic dinosaurian bipedality arose in the 1990s (see above). With the exemption of Riggs (1904), the first attempts to reconstruct stance and locomotion in single sauropodomorph genera were strongly influenced by the former view. For example, Hay (1908, 1910, 1911) and Tornier (1909) assumed the locomotion of *Diplodocus* to be crocodile-like, with sprawling limbs and the belly resting on the ground, hardly able to move effectively on land. Abel (1910), Holland (1910), and Matthew (1910) rejected these extreme views and argued for an upright, graviportal stance, but the idea of a semi-aquatic mode of life that helped these animals to bear their enormous weight persisted in the literature for the next 50 years (e.g., Colbert, 1962; Romer, 1966). Janensch (1937) suggested that *Brachiosaurus* may have fed on high trees, but did not go so far as to reject a semi-aquatic lifestyle. The paradigm shift did not come until the works of Bakker (1971) and Coombs (1975, 1978a), who reinterpreted sauropod anatomy and established the modern view of active, fully terrestrial herbivores.

From this point onwards, further interpretations of sauropod functionality were possible. Using equations based on biomechanical works on extant mammals, Alexander (1976, 1985, 1989) and Thulborn (1982) reconstructed speeds and general gaits in dinosaurs, including sauropodomorphs. According to these analyses, sauropods possessed athletic capabilities similar to elephants, but reached lower speed:mass ratios than modern mammals. Moreover, the speed of sauropods was found to be primarily controlled by step length and step frequency of the forelimbs. The works of Alexander and Thulborn remained the only accounts on sauropod locomotor behavior until Christiansen (1997a) compared sauropod limbs to that of elephants in some detail and interpreted their functional morphology. He found similarities in both groups, such as the dominant role of proximal retractors in locomotion, while forearm extensors lost their importance. Christian et al. (1999a,b) recalculated the speeds of sauropods and forelimb biomechanics of *Brachiosaurus* with improved biomechanical methods, while Wilson and Carrano (1999) were the first to integrate ichnological, morphological and biomechanical evidence to show that wide-gauge sauropod trackways were produced by titanosaurs, a sauropod subgroup with specialized locomotor adaptations. Carrano (2000) studied the functional morphology of hindlimbs in dinosaurs and noted that the improved, parasagittal stance and gait evolved independently in several dinosaur lineages, including sauropods. Bonnan (2003, 2004) was the first author who dealt with the evolution of sauropod forelimb functional morphology in detail. He recognized that full pronation of the manus was not possible in sauropods and suggested a close connection between a triradiate morphology of the proximal ulna and a tube-like metacarpus. However, he later changed his view regarding the latter point and now assumes that both characters evolved independently (Bonnan and Yates, 2007). Bonnan (2005) also gave an account on the functional evolution of the pes in sauropods. Most recently, Carrano (2005) analyzed the evolution of proportions and orientations of the individual limb elements in sauropodomorphs and listed adaptations in connection with graviportal stance in sauropods, including a vertically oriented metacarpus and elongate intermetacarpal articulations. He comes to the same conclusions as Christiansen (1997a): the importance of flexion and extension of the distal limb elements for locomotion was reduced, and the main propulsive motion was performed by the proximal elements (humerus and femur). None of the works listed above includes detailed soft tissue reconstructions or a large taxon sample size.

The phylogenetic interrelationships of sauropods are well understood due to recent works. During the last decade numerous cladistic analyses of sauropods were published that clarified sauropod interrelationships (Upchurch 1995, 1998, 1999; Calvo and Salgado, 1995; Salgado et al., 1997; Wilson and Sereno 1998; Wilkinson et al., 2000; Curry Rogers and Forster, 2001; Wilson 2002; Upchurch et al., 2004). Although these works differ in some details, a consensus emerged that basal sauropods form a set of successive sister taxa to a monophyletic group called Neosauropoda, which split prior to the Upper Jurassic into two main lineages, Diplodocoidea and Macronaria (fig. 1-2).

Apart from studies of sauropodomorphs, important contributions to the understanding of dinosaur forelimb morphology and soft tissue anatomy were made in other fields. Although the methodology of phylogenetic inference (chapter 2) was formalized only recently (Bryant and Russell, 1992; Witmer, 1995), accompanied by the establishment of the name ‘Extant Phylogenetic Bracket’ (EPB) by Witmer (1995), Gregory and Camp (1918) and Miner (1925) already applied a similar method for their reconstructions of musculature of the cynodont therapsid *Cynognathus* and the temnospondyl amphibian *Eryops*, respectively. Muscle reconstructions of early synapsids were also performed by Romer (1922), who furthermore reconstructed pelvic muscles in saurischians, mainly based on the anatomy of crocodilians (Romer, 1923). Later workers did not explicitly state their methods for reconstructing limb muscles in dinosaurs, e.g. in Russell's (1935) reconstruction of the ceratopsian *Chasmosaurus*. There were no further attempts of dinosaur muscle reconstructions, until Colbert (1964) in his overview of saurischian interrelationships also considered the pelvic musculature as an important difference between the two major saurischian subgroups. Shortly thereafter, Ostrom (1969, 1974, 1976) included muscle reconstructions combined with functional interpretations in his groundbreaking description of the advanced theropod *Deinonychus* and his hypothesis of the origin of bird flight. Other workers began to include forelimb muscle reconstructions in studies of extinct synapsids (Jenkins, 1971; Walter, 1986), captorhinids (Holmes, 1977) and dinosaurs (Raath, 1977; Coombs, 1978b; Santa Luca, 1980; Nicholls and Russell, 1985; Dilkes, 2000; Carpenter, 2002). With respect to dinosaurs, most of these works were either based on avian or crocodilian anatomy, without clear phylogenetic bracketing. Bryant and Seymour (1990) evaluated the reliability of various reconstructions and criticized that in recent contributions dinosaur muscles were modeled on bird anatomy only, an observation that finally led to the development of the EPB (see above). Finally, Farlow et al. (1995) summarized the results and problems of previous analyses of dinosaurian muscle architecture.

The 1990s brought a change in methodology of muscle reconstructions in extinct vertebrates, not only by introduction of the EPB, but also by a new phylogenetic perspective on muscle change that complements reconstructions of single genera (or specimens). With respect to saurischians, most workers concentrated on theropod hindlimb musculature. Gatesy (1990) opened the debate by his account on the evolution of the M. caudofemoralis longus in theropods, and was followed by others (Gatesy, 1995, 2001, 2002; Gatesy and Middleton, 1997; Farlow et al., 2000; Hutchinson and Gatesy, 2000; Hutchinson, 2001a,b, 2002, 2004; Hutchinson et al., 2005). Other applications of the EPB deal with the evolution of parts of the cranial soft tissue in archosaurs (Witmer, 1997; Holliday and Witmer, 2007). Finally, Jasinoski et al. (2006) were the first to apply a similar approach to forelimbs in a group of theropods (dromaeosaurids). While a detailed understanding of evolutionary transformations of both myology and osteology of the limbs is beginning to emerge for the theropod-bird transition, this field is hardly covered in other groups of dinosaurs.

Outline of this work

The research presented in this work is part of the subproject C4, 'Evolution of the sauropod *bauplan*', within the DFG Research Group 533. Project C4 focused on the interrelationships of the sauropodomorph dinosaurs (PIs Rauhut, Hone) and the evolution of the appendicular skeleton and musculature. To gain a view on sauropod limb evolution that is as complete as possible, it was necessary to examine a high number of taxa that represent the entire evolutionary pathway from basal archosaurs to neosauropods. For these reasons, and for the significant differences between forelimbs and hind limbs, the complex question of locomotor evolution in sauropods has been subdivided into two separate, but closely related projects. Regina Fechner examined the evolution of the hind limb complex, whereas the work at hand explores the evolution of the pectoral girdle and forelimb in sauropodomorphs, dealing with following questions: Which transformations occurred during sauropodomorph evolution, and when? Is it possible to identify key adaptations or preadaptations in both the skeleton and the musculature that give clues to sauropod gigantism? Based on osteology and myology, which functional changes in the forelimb can be inferred on the line to neosauropods?

Although accounts on saurischian forelimb functional morphology and reconstructions of dinosaurian forelimb musculature have been published before (see above), this work provides scientific novelties in two different aspects: a broad phylogenetic approach that examines forelimb functional adaptations and transformations throughout sauropodomorph evolutionary history (instead of accounts on single genera), and for the first time reconstructions of appendicular soft tissue anatomy in this group. Moreover, among works that deal with dinosaur locomotor evolution, in most cases the forelimb is neglected, possibly due to the bipedality paradigm mentioned above. Although many ornithischians are also obligate or facultative quadrupeds (stegosaurs, ankylosaurs, advanced ceratopsians, some advanced ornithopods), this work is the first that examines the importance of forelimb evolution under the broader context of quadrupedal locomotion in dinosaurs.

The main text starts with a chapter on ‘Material and Methods’, listing the fossil material, extant specimens and bibliographic resources that serve as the primary data source for this work, and explaining the methods applied, especially the Extant Phylogenetic Bracket (EPB). In chapter 3, all archosaur forelimb muscles are reviewed, and the possible inference in the archosaurian ancestor is evaluated for each muscle. This is a necessary prerequisite for the reconstructions done in the following chapters, since no standardized concept of osteological and myological nomenclature for fossil tetrapods currently exists. Various scholars use different nomenclatorial concepts that often make individual works difficult to compare.

Therefore, chapter 3 attempts to establish a nomenclatorial consensus for archosaurian forelimb myology, which may serve as a base for future descriptions and reconstructions in crurotarsians, pterosaurs and dinosaurs. The following five chapters are case studies of muscle reconstructions and functional morphology of several fossil taxa. The forms chosen represent different stages on the evolutionary line to Neosauropoda. Chapter 4 describes *Euparkeria capensis*, a form close to the crocodile-bird split and therefore serving as the archetype for all archosaurs, and the basal dinosauriform *Lewisuchus admixtus*. Chapter 5 deals with several representative dinosaurs that lie outside Sauropodomorpha, such as basal ornithischians, herrerasaurids, and basal theropods, and reviews the evidence for plesiomorphic bipedalism in dinosaurs. Forms on the stem-line of sauropodomorphs, such as *Saturnalia tupiniquim* and *Thecodontosaurus antiquus*, are addressed in chapter 6. Forelimb functional morphology and myology of ‘typical prosauropods’ are evaluated in chapter 7, with a study on different adaptational pathways within this group. Chapter 8 deals with forelimb anatomy and functionality in basal sauropods and gives an outlook on further modifications in neosauropods. Finally, chapter 9 integrates the details accumulated in the preceding chapters by use of a phylogenetic framework, and summarizes the anatomical transformations that led to the evolution of the sauropod forelimbs. A short summary of the main results of this work is given in chapter 10.

2 Material and Methods

Material

The primary data source of this work is, of course, original fossil material. In order to trace evolutionary transformations of sauropodomorph forelimb osteology and musculature in detail, it was necessary to examine as much relevant fossils as possible. Therefore, skeletal remains of at least 100 individuals of about 48 different genera have been examined in scientific collections worldwide. These numbers have to be given with an expression of uncertainty, because in some cases the author noted unclear or incorrect taxonomic assignments. In course of this work, it became clear that a general taxonomic revision of basal dinosauromorphs and sauropodomorphs is necessary, a task clearly beyond the scope of this thesis. However, results from the author's own examinations will be incorporated into a monographic work that covers a complete taxonomic revision of the Saurischia (Rauhut et al., in prep.).

The following taxa were examined personally (in phylogenetic order):

- basal Archosauria: *Euparkeria capensis*
- basal Ornithodira: *Scleromochlus taylori*, *Lagosuchus talampayensis*, *Lewisuchus admixtus*, *Marasuchus lilloensis*
- basal Saurischia: *Eoraptor lunensis*, *Herrerasaurus ischigualastensis*, *Guaibasaurus candelariensis*, *Saturnalia tupiniquim*
- basal Neotheropoda: *Dilophosaurus wetherilii*, *Coelophysis bauri, Segisaurus halli, Liliensternus liliensterni, Ceratosaurus nasicornis, Piatnitzkysaurus floresi, Kaijiangosaurus lini, Poekilopleuron bucklandii*
- non-sauropodous Sauropodomorpha: *Thecodontosaurus antiquus, Efraasia minor, Plateosaurus engelhardti, Ruehleia bedheimensis*, *Unaysaurus tolentinoi*, undescribed prosauropod ('*Riojasaurus*') from the Los Colorados Formation, second undescribed prosauropod (PVL field number 6) from the Los Colorados Formation, *Coloradisaurus brevis, Riojasaurus incertus, Plateosauravus cullingworthi* ('*Euskelosaurus*'), *Mussaurus patagonicus*, undescribed prosauropod ('*Plateosaurus* sp.') from the El Tranquilo Formation, *Massospondylus carinatus*, *Lufengosaurus huenei, 'Gyposaurus' sinensis, Yunnanosaurus huangi*
- non-eusauropod Sauropoda: *Anchisaurus polyzelus*, undescribed sauropod ("*Melanorosaurus*") from the Lower Elliot Formation, *Melanorosaurus readi*, *Antetonitrus ingenipes*, *Kotasaurus yamanpalliensis*

- Eusauropoda: *Shunosaurus lii*, *Barapasaurus tagorei, Klamelisaurus gobiensis, Omeisaurus tianfuensis, “Bashunosaurus kaijiangoensis”, Mamenchisaurus constructus, M. hochuanensis, M. guangyuanensis, Cetiosauriscus leedsi*, *Patagosaurus fariasi, Cetiosaurus oxoniensis, “Cetiosaurus” mogrebiensis, Bellusaurus sui*

A complete list of the material examined is given in Table 2-1.

Table 2-1

Taxon name (number of individuals)	**Specimen numbers**
Anchisaurus polyzelus (4)	UCMP 82961 YPM 1883 YPM 208 YPM 209
Antetonitrus ingenipes (2)	BP/1/4952 BP/1/4952b
Barapasaurus tagorei (≥1)	ISI R 86 ISI R 69 ISI R unnumbered coracoid
‘Bashunosaurus kaijiangoensis’ (1)	CUT unnumbered
Bellusaurus sui (≥1)	IVPP field site 83003
Ceratosaurus nasicornis (1)	USNM 4735
Cetiosauriscus leedsi (1)	BMNH R 3078
Cetiosaurus oxoniensis (1)	OUMNH J 13605-13607 OUMNH J 13609-13613
‘Cetiosaurus’ mogrebiensis (2)	MNHN No. 3 MNHN No. 8
Coelophysis bauri (7)	AMNH 7223 AMNH 7224 AMNH 7227 AMNH 7228 AMNH 7230 AMNH 7231 AMNH 7238
Coloradisaurus brevis (≥2)	PVL 3967
Dilophosaurus wetherili (2)	UCMP 37302 UCMP 77270
Efraasia minor (7)	SMNS 12354 SMNS 12667 SMNS 12668 SMNS 12684 SMNS 12843 SMNS 14880 SMNS 14881 SMNS 17928
Eoraptor lunensis (1)	PVSJ 512
Euparkeria capensis (4)	SAM 5867 SAM 6047 SAM 7696 SAM 7700

Table 2-1 (continued)

Guaibasaurus candelariensis (1)	MCN-PV 2355 MCN-PV 2356
'Gyposaurus' sinensis (1)	IVPP V26
Herrerasaurus ischigualastensis (6)	MACN 18060 MLP 61-VIII-2-3 (currently in MACN) PVSJ 53 PVSJ 373 PVSJ 407 PVSJ 605
Kaijiangosaurus lini (1*)	CUT 13655
Klamelisaurus gobiensis (1)	IVPP V9492
Kotasaurus yamanpalliensis (≥5)	BSC unnumbered GSI-SR 70/SY GSI-SR 71/SY GSI-SR 72/SY GSI-SR 73/SY
Lagosuchus talampayensis (2)	MCZ 9483 (= 'MCZ 4121') PVLR 09
Lewisuchus admixtus (1)	PVLR 01 (= MLP 64-XI-14-6)
Liliensternus liliensterni (≥2)	MB.R.2175
Lufengosaurus huenei (1)	IVPP V15
Mamenchisaurus constructus (1)	IVPP 946
Mamenchisaurus hochuanensis (1)	ZDM 0126
Mamenchisaurus guangyuanensis (1)	CUT unnumbered
Marasuchus lilloensis (2)	PVL 3871 (currently in MACN) PVL 4672 (currently in MACN)
Massospondylus carinatus (5)	BP/1/4934 BP/1/4998 BP/1/5241 SAM 3357 (*'Gryponyx africanus'*) SAM K391
Melanorosaurus readi (≥3)	NM 3314 SAM-PK-3449 SAM-PK-3532
Mussaurus patagonicus (1)	PVL 4210 (currently in MACN)
Omeisaurus tianfuensis (1)	ZDM 5002
Patagosaurus fariasi (3)	MACN CH-225 MACN CH-932 PVL 4617
Piatnitzkysaurus floresi (2)	MACN CH-895 PVL 4073
Plateosauravus cullingworthi (≥2)	SAM 3341-3351
Plateosaurus engelhardti (4)	GPIT 1 GPIT 2 SMNS 13200
Poekilopleuron bucklandii (1)	MNHN 1897-2
Riojasaurus incertus (1)	PVL 3808
Ruehleia bedheimensis (1)	MB RvL 1
Saturnalia tupiniquim (2)	MCP 3844-RV (currently in FFCLRP) MCP 3845-RV (currently in FFCLRP)
Scleromochlus taylori (1)	BMNH R3146 BMNH R3556 BMNH R3914 BMNH R4823/4
Segisaurus halli (1)	UCMP 32101
Shunosaurus lii (1)	IVPP V9065

Table 2-1 (continued)

Thecodontosaurus antiquus (2)	YPM 2192 YPM 2195
Unaysaurus tolentinoi (1)	UFSM 11069 (currently in MN)
Yunnanosaurus huangi (1)	IVPP V20
Undescribed prosauropod from the Los Colorados Fm	PVL field number 6
Undescribed prosauropod from the Los Colorados Fm	PVLR 056 ('*Riojasaurus*')
Undescribed prosauropod from the El Tranquillo Fm	MLP 68-II-27-1 (currently in MACN, '*Plateosaurus*') MACN SC-3379
Undescribed prosauropod from the Lower Elliot Fm	NM 1551 ('*Melanorosaurus*')

Table 2-1. Alphabetical list of fossil taxa examined in this work. Specimen counts are given in parentheses behind the taxon binomen. **Kaijiangosaurus lini* is a composite of at least three individuals; however, all forelimb elements appear to belong to the same individual.

In addition to the fossil material, three specimens of extant archosaurs were obtained for dissection, including *Caiman crocodilus* (1) and *Gallus gallus* (2). Furthermore, macerated skeletons of *Crocodylus porosus*, *Alligator mississippiensis*, *Gavialis gangeticus*, *Gallus gallus*, and *Gyps fulvus* were investigated for osteological correlates of the musculature (see below, Methods).

Methods

All fossil bones were visually examined and described in high detail. Special attention was given to the structure of bone surfaces. Ridges, tubercles, depressions, rugosities, and striations were carefully described and mapped in sketches. If possible, series of digital photographs, mostly stereo pictures of 4.0 megapixels resolution, were taken for all sides of each element. Furthermore, a series of straight distance measurements was taken for each element by use of standard calipers and tape measures (fig. 2-1). Based on descriptions, drawings, photographs, and measurements, digital images of single elements and articulated skeletal parts were created using Adobe® Illustrator® CS2 and Adobe® Photoshop® CS2 computer programs. For better comparison, all drawings show elements of the right body side. If drawings are based on elements from the left body side, the images were mirrored.

The muscle reconstructions presented in the following chapters are mainly based on a thorough review of the literature on tetrapod (especially archosaurian) forelimb muscles (chapter 3). To confirm and three-dimensionally visualize the findings of previous workers, own dissections of the crocodilian *Caiman crocodilus* and the chicken *Gallus gallus* were made. During these dissections, special attention was given to potential osteological correlates of individual muscles, such as ridges, tubercles, depressions, rugosities, striations, and other surface properties. These findings were counter-checked with macerated skeletons of various other archosaurs (see above, Material) and descriptions in the literature. The sum of these data forms the basis for the application of the Extant Phylogenetic Bracket (see below). As for the osteological images, digital drawings of reconstructed musculature were created by using Adobe® Illustrator® CS2.

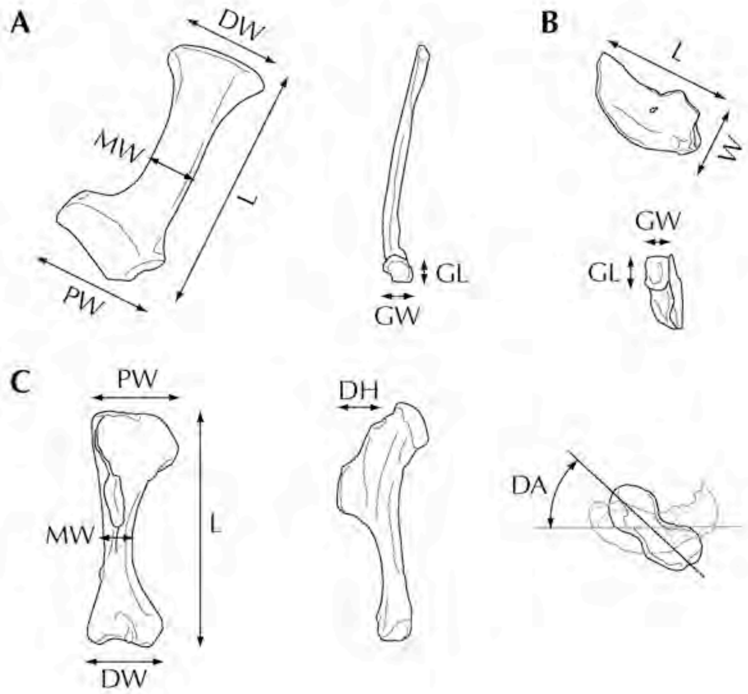

Figure 2-1. Measurements taken during examination of original material. **A**, scapula. **B**, coracoid. **C**, long bones. Abbreviations: DA, deflection angle; DH, deltopectoral crest height; DW, distal width; GL, glenoid length; GW, glenoid width; L, length; MW, mid-shaft width; PW, proximal width; W, coracoid width.

The Extant Phylogenetic Bracket (EPB) is a rationale formally established by Witmer (1995) and consistently applied for soft tissue reconstructions throughout this work. It might be noted that Bryant and Russell (1992) already published a similar methodology, but did not create a formal name. Both approaches try to minimize the amount of speculation in attempts of soft tissue reconstructions in extinct vertebrates by a strict deductive concept based on phylogenetic inference. Frost (1990) and Witmer (1995) emphasize that the form of a bone actually is induced by the morphology of the surrounding soft tissues and the biomechanical stress they exert on the bone, not vice versa. Therefore, accurate soft tissue reconstructions are the basis for any interpretations of the function and biology of an extinct organism, of interaction of extinct organisms, and of long-lost ecosystems. Otherwise, inaccuracies in soft tissue reconstructions of a certain organ will cause false functional interpretations, which in turn may lead to increasing errors in the interpretation of the biology of whole organisms and their ecology.

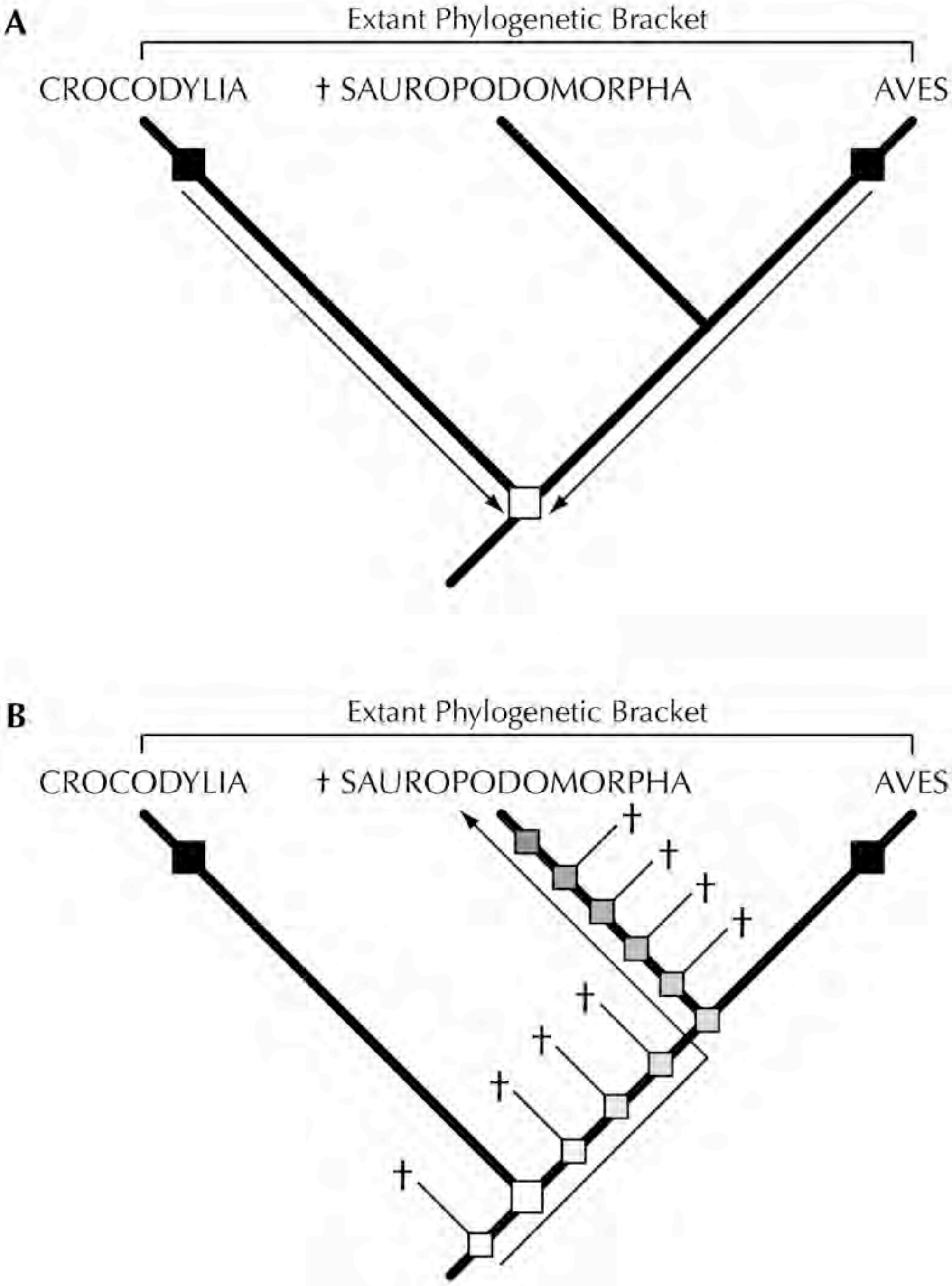

Figure 2-2. The Extant Phylogenetic Bracket as applied in the present work. **A**, Identification of homologous muscles and their osteological correlates in extant archosaurs; based on these data, reconstruction of the musculature of their last common ancestor. **B**, Tracing of transformations of osteological correlates during sauropodomorph evolution and inference of myological change.

The main work steps for phylogenetic inference of muscles, based on the rationales of Bryant and Russell (1992) and Witmer (1995), are shortly summarized here:

- identification of the closest extant outgroups to the extinct taxon of consideration; these taxa form the Extant Phylogenetic Bracket (fig. 2-2A)
- verification of muscle homologies in both extant taxa by outgroup comparison (see chapter 3)
- identification of osteological correlates (textural traces left by muscles on a bone) of individual muscles
- identification of homologous osteological correlates in the fossil taxon of consideration
- reconstruction of origin and insertion of each muscle according to the identified osteological correlates
- reconstruction of attachment sites of muscles that have no osteological correlates, based on phylogenetically inferred plesiomorphic origins and insertions and their relationships to other muscles
- inference of line of action of each muscle

Regarding the last step, reliant reconstructions of two- or three-dimensional forms of muscles in extinct vertebrates are impossible by modern knowledge, and are therefore pure speculation (see Gans and Bock, 1965; McGowan, 1979, 1982, 1986; Bryant and Seymour, 1990). Accordingly, this work refrains from such attempts and provides only lines of action in a three-dimensional space that span between points or areas of origin and insertion. This is scientifically more founded, however not free from extrapolation (see chapter 3 for a detailed discussion of this issue).

For this work, the procedure described above was applied to as much non-neosauropod sauropodomorph taxa as possible. Furthermore, close outgroups such as dinosauriforms, herrerasaurids and basal theropods are also taken into account (fig. 2-2B). The osteological, myological and morphometric differences observed are then ordered with the help of cladograms and stratocladograms to determine the exact sequence of evolutionary modifications, their point of time, and if possible, their geographical distribution. The phylogeny used for creation of these diagrams is a combination of overlapping published phylogenies (see chapter 9), because no single analysis currently exists that covers all taxa examined in this work.

Osteological nomenclature

Osteological terms used in this thesis are mainly based on Romerian nomenclature and chiefly follow the convention of the book ‘The Dinosauria’, second edition (Weishampel et al., 2004). Replacement of Romerian terminology by standardized terms of the Nomina Anatomica Avium (NAA; Baumel et al., 1993) is avoided whenever possible (*contra* Harris, 2004), because the highly specialized morphology of the avian forelimb can hardly serve as a nomenclatorial model for more plesiomorphic tetrapods such as sauropods. For a detailed discussion on the advantages and disadvantages of applying the NAA to all diapsids, see Wilson (2006). However, in some cases Romerian nomenclature is imprecise or misleading, and specifications of such terms as suggested in the following chapters are in part based on the NAA. Nevertheless, a convention completely adopted from the NAA throughout this work is the use of the terms cranial/caudal instead of anterior/posterior. The main reasons are that the NAA standardization of myological nomenclature is an advancement over the proliferation of myological synonyms in the decades before, and that there is no conflict with traditional paleontological terms. Accounts on musculature of fossil vertebrates use highly differing nomenclatorial systems that in most cases are based on extant model taxa anyway (chapter 3). Therefore, to keep compatibility with NAA myological terms (e.g., M. serratus superficialis pars cranialis), the use of anterior/posterior has been abandoned and topographical attributes of common Romerian terms have been exchanged accordingly (e.g., 'cranial process of ulna' instead of 'anterior process'). A conflict with standardized terminology of saurischian vertebral laminae as established by Wilson (1999) is not given since these structures do not play a role for the topics discussed in this thesis.

Another terminological problem is the orientation of the scapulocoracoid and humerus in extinct archosaurs. Reconstructions of the shoulder girdle in sauropods reach from horizontal (e.g., Parrish and Stevens, 2002) to steeply inclined orientations (Schwarz et al., 2007a), creating confusingly different usages of topographical attributes. For instance, the distal tip of the scapular blade may either be termed 'caudal end' or 'dorsal end'. Likewise, the humerus changed its orientation during archosaur evolution, from a plesiomorphical semi-erect position to an upright orientation in sauropods (chapters 4–9); therefore, the plesiomorphical dorsal side of the humerus later became the posterolateral side (fig. 2-3). In their account on dromaeosaurid shoulder musculature, Jasinoski et al. (2006) avoided these problems by consistently applying *developmental* topographical attributes. Since the orientation of the developing limb is similar in all tetrapod embryos, this concept avoids confusion when changes of muscular attachment sites are discussed. However, the functional orientation of each element sometimes differs strongly from its developmental orientation (tab. 2-2).

Therefore, strict usage of developmental topographical attributes hampers functional interpretations, which yet are the main purpose of the present study. Accordingly, the solution applied here is to use generally developmental orientations (tab. 2-2), but also to discuss functional orientations when necessary.

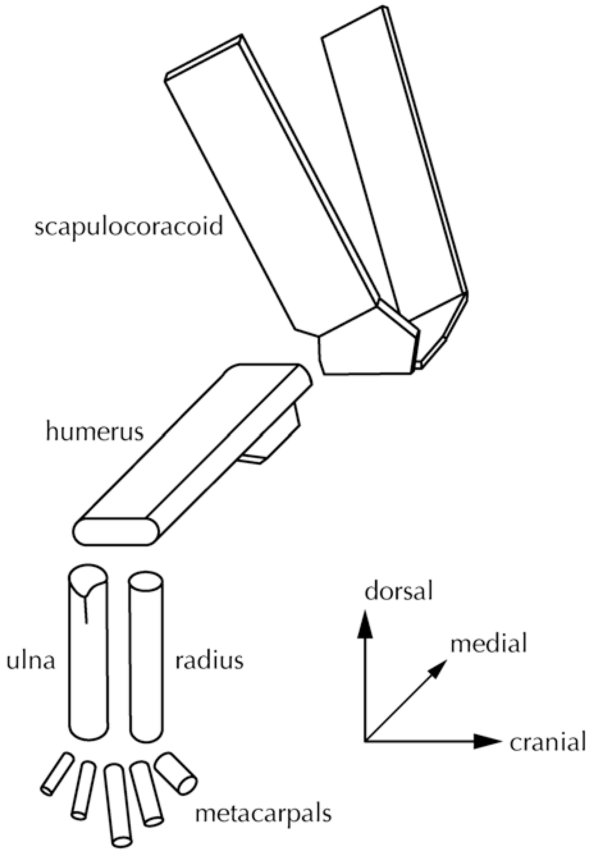

Figure 2-3. Simplified diagram of the developmental orientation of sauropodomorph forelimb elements. Compare with Table 2-2.

Table 2-2

Element	Developmental orientation	Functional (positional) orientation			
		Basal sauropodomorphs		**Higher Sauropods**	
		This work	Galton and Upchurch (2004)	This work	Upchurch et al. (2004)
Scapula	dorsal	caudodorsal	dorsal	caudodorsal	caudal
	ventral	cranioventral	ventral	cranioventral	cranial
	anterior	craniodorsal	cranial	craniodorsal	dorsal
	posterior	caudoventral	caudal	caudoventral	ventral
	lateral	lateral	lateral	lateral	lateral
	medial	medial	medial	medial	medial
Coracoid	dorsal	dorsolateral	dorsal	caudolateral	caudal
	ventral	ventromedial	ventral	craniomedial	cranial
	anterior	cranial	cranial	craniodorsal	dorsal
	posterior	caudal	caudal	caudoventral	ventral
	lateral	ventrolateral	lateral	craniolateral	lateral
	medial	dorsomedial	medial	caudomedial	medial
Humerus	dorsal	dorsolateral	caudal	caudolateral	caudal
	ventral	ventromedial	cranial	craniomedial	cranial
	anterior	cranial	lateral	craniolateral	lateral
	posterior	caudal	medial	caudomedial	medial
Radius	anterior	craniolateral	lateral	cranial	cranial
	posterior	caudomedial	medial	caudal	caudal
	lateral	caudolateral	caudal	lateral	lateral
	medial	craniomedial	cranial	medial	medial
Ulna	anterior	craniolateral	lateral	cranial	cranial
	posterior	caudomedial	medial	caudomedial	caudal
	lateral	caudolateral	caudal	caudolateral	lateral
	medial	craniomedial	cranial	craniomedial	medial
Metacarpalia	dorsal	dorsal	cranial	cranial	cranial
	ventral	palmar	caudal	palmar	caudal
	anterior	medial	medial	medial	medial
	posterior	lateral	lateral	lateral	lateral

Table 2-2. Comparison of developmental and functional orientations and corresponding topographical attributes in the pectoral girdle and forelimb of sauropodomorphs. The functional orientation as applied throughout this work is also compared to that applied in the most recent reference works on sauropodomorph anatomy, as published in The Dinosauria (Weishampel et al., 2004).

3 A review of archosaurian forelimb musculature: The fundament for reconstructions in extinct taxa

Introduction

The extremities of tetrapods are highly complex structures. With regard to the archosaur forelimb, plesiomorphically 31 individual bones (humerus, radius, ulna, carpals, metacarpals, phalanges) articulate in three major (shoulder, elbow, wrist) and numerous minor (radioulnar, intercarpal, carpometacarpal, metacarpophalangeal, interphalangeal) joints. The forelimb articulates with the trunk via the pectoral girdle, which consists of three major elements (scapula [including suprascapula], coracoid, clavicles). Soft tissue connects the pectoral girdle to the cervical and cranial dorsal vertebral column, and to the dorsal and sternal ribs. The ventral pectoral girdle (i.e., the coracoid) articulates with the sternum.

These bony and cartilaginous elements are supported and controlled by numerous skeletal muscles. Ligaments also have a significant influence of joint movement (Alexander and Bennett, 1987), but are hard to reconstruct since they usually lack unambiguous osteological correlates (see Jenkins, 1993). Therefore, the soft tissue inference throughout this thesis focuses on the musculature. Due to reductions or development of additional muscular heads, the exact number of individual muscles varies among taxa (or sometimes, individuals). Nevertheless, around 70 individual skeletal muscles in 43 muscle groups probably existed in the forelimb of basal archosaurs. The number of scholars who studied the forelimb musculature of birds, crocodiles, and other diapsids may be in the same order of magnitude, and these various authorities often adopted different nomenclatorial systems (see Davis, 1936). These inconsistencies in terminology are not problematic for the description of the myology of individual species, genera, or small groups of closely related species, but they become disturbing in attempts to reconstruct musculature in a major extinct clade, using the rationale of phylogenetic inference as proposed by Bryant and Russell (1992) and Witmer (1995).

Currently, there is a debate about standardizing osteological and myological nomenclature in amniotes by abandoning Romerian terms and extending existing standardized terminologies to all stem-taxa: The veterinarian NAV (Nomina Anatomica Veterinaria, International Committee on Veterinary Anatomical Nomenclature, 1994) is put forward as the standard nomenclature for all synapsids, and the NAA (Nomina Anatomica Avium, Baumel et al., 1993) as the standard nomenclature for all diapsids (Harris, 2004). However, this concept generates several logical and practical problems (Wilson, 2006), and is currently not widely accepted. One of the purposes of this chapter is therefore to propose a nomenclatorial system for diapsid (especially archosaurian) forelimb myology that keeps compatibility with major classical works, but incorporates NAA concepts when necessary to avoid ambiguities.

However, due to the major morphological gaps between extant archosaurian clades, it is currently not possible to homologize all forelimb muscles with certainty. These cases and their impact on attempts to reconstruct musculature in extinct taxa are also discussed. A third question to be explored in this chapter is the meaningfulness of phylogenetic inference, if the 'bracket taxa' of the EPB are morphologically and temporally so distant like birds, crocodilians, and more basal diapsids. In short, this chapter examines theoretical aspects of phylogenetic inference of extinct archosaur forelimb musculature, and therefore forms the logical fundament for the reconstructions presented in the following chapters.

General theoretical aspects of phylogenetic inference of musculature

The methodological basis for muscle reconstructions in extinct taxa is the Extant Phylogenetic Bracket (EPB) as proposed by Bryant and Russell (1992) and Witmer (1995). The concept of the EPB has already been described under 'Material and Methods' (chapter 2). Here, the practical application of the EPB for the reconstruction of archosaur forelimb muscles will be explored shortly.

In tetrapods, there are basically three different ways for a muscle to connect to the skeleton and exert force on it: direct (fleshy), tendinous, and aponeurotically via tendon-like sheets of connective tissue that attach to a wider area or linear along the bone (Dolgo-Saburoff, 1929; Hildebrand and Goslow, 2001). Bryant and Seymour (1990) examined the correlation of attachment type and potential osteological correlate, based on a case study in mammalian carnivores. These authors found that muscles with a direct type of attachment to the bone are less likely to have osteological correlates. Such muscles are sometimes associated with depressions or flattened surfaces on the bone, but areas of these bone surface features do not necessarily correlate with areas of muscle attachment (Bryant and Seymour, 1990). However, the border between areas of attachment of two neighboring muscles may be marked in some cases by a low intermuscular ridge. Likewise, parallel orientations of near-surface Sharpey's fibers may also give a hint towards the extent of a fleshy muscular attachment. In fossil bones, fiber orientation is often indicated by faint, parallel surface striations, or is directly visible due to erosion of the outermost bone layer. In contrast to direct attachments, tendons and aponeuroses more commonly have osteological correlates. Tendons often form scars or pits with reduced pore density, while aponeuroses in most cases leave distinct scars on the bone (Bryant and Seymour, 1990). Similar structures are also associated with ligaments. Scarring is explained by ossification of collagen fibers above the bone surface, a physiological reaction to tensile stress (Jones and Boyde, 1974). Bryant and Seymour (1990) also noted that tendinous and aponeurotic attachments are more abundant in mammals than in archosaurs, which may explain why muscle reconstructions in extinct archosaurs are less reliable than in extinct mammals (see McGowan, 1979, 1982, 1986). Although the attachment types of a certain muscle may vary among closely related taxa or even intraspecifically, some muscles are relatively conservative in this respect (see muscle descriptions below).

Due to the ambiguities produced by relative specialization of or variation within crown-group taxa (see below), it is not possible to phylogenetically infer origin and insertion for all muscles in extinct taxa with certainty. Witmer (1995) categorized the quality of soft tissue reconstructions into three 'levels of inference'.

In the ideal case, both extant outgroup taxa possess a homologous soft tissue attribute (a muscle) that is consistently associated with osteological correlates. If these correlates can be recognized in fossils, phylogenetic inference is unequivocal ('Level I inference') and supports reconstruction of this feature in the extinct taxon. For example, M. triceps brachii caput scapulare is present in crocodilians and in birds (NAA term: M. scapulotriceps), and is associated with distinct osteological correlates (origin: scar dorsal to the glenoid, insertion: olecranon process). Because both correlates are also present in basal archosaurs, the muscle is likely to have existed in these forms as well. However, there is also the possibility that a muscle does not leave any clear osteological correlate in both extant bracket taxa, but that a conspicious structure is present at the probable site of origin or insertion of this muscle in the extinct group of interest. To interpret this structure as an osteological correlate of a certain muscle involves more speculation than 'normal' level I inference. (Regarding sauropodomorph forelimb evolution, the rare cases where such an interpretation becomes necessary will be discussed in the following chapters.)

A 'Level II inference' is given if one of the extant outgroup taxa lacks a certain muscle, either due to its plesiomorphic anatomy or due to apomorphic reduction. For example, M. levator scapulae is plesiomorphically present in crocodilians, but completely lost in birds. Based on the plesiomorphic form of the scapula in basal archosaurs, it is reasonable to infer the presence of M. levator scapulae in these forms, too. However, this inference involves more speculation, because the EPB assessment is equivocal in this case.

Finally, even more speculation is involved when features are reconstructed that are not present in both extant bracket taxa ('Level III inference'). For example, it was frequently suggested that sauropodomorphs possessed extensive, vascularized cartilaginous epiphyses and large articular capsules (Hay, 1911; Holliday et al., 2002; Schwarz et al., 2007b), osteologically correlated to the rough, pitted articular surfaces of the long bones. However, no such structure exists in crocodiles or birds, and the EPB assessment is negative with respect to this feature.

An assessment of the presence of each forelimb muscle in basal archosaurs is given below, with an indication of the level of inference where necessary. Naturally, level III inferences of muscles are avoided throughout this thesis.

Variation and the choice of extant sample taxa

The uncertainty of phylogenetic inference increases with the temporal and morphological distance between both extant bracket taxa, especially if the matter of interest is not only the mere existence of a muscle, but its exact location. This uncertainty becomes even stronger if the extant bracket taxa are themselves heterogenic groups with much interspecific variation. Single specimens of one extant bracket taxon may not be representative for the whole clade. Moreover, they may show homoplastic characters that are also present in the second extant bracket taxon, which may cause false interpretations of symplesiomorphic anatomy. Therefore, the ideal would be to reduce variations observed within each extant bracket taxon to a 'consensus anatomy' that represents the plesiomorphic condition, which may then serve as a base for the EPB assessment. However, due to missing anatomical and phylogenetic data in many taxa, this is a challenging task. Two examples of this problem are given in the following.

Numerous anatomical studies of modern birds exist, but recent accounts on crocodilian forelimb anatomy are relatively rare. Meers (2003) published the sole comparative study, incorporating dissections of 10 specimens of five different species (genera *Alligator, Crocodylus, Gavialis,* and *Osteolaemus*). He found crocodilian forelimb muscles to be highly conservative, but there is some intraspecific variation in the locations and types of attachment of several shoulder muscles. Meers (2003) observed the greatest interspecific variation in *Gavialis gangeticus*, an aquatic species that exhibits displacement of forearm extensors and flexors, relative to the condition found in other crocodilians. He suggested that these modifications are a consequence of the aquatic mode of life and locomotion in *Gavialis*. However, Jasinoski et al. (2006), who based their study about forelimb musculature in dromaeosaurids on dissections of several specimens of *Caiman*, provided muscle insertion maps that differed from those of Meers (2003). For example, while Meers (2003) found M. cucullaris ('M. trapezius' in his work) to insert on the cranial edge of the scapular blade in all examined species, this muscle attaches to the dorsal edge of the acromial region in *Caiman*, resembling the plesiomorphic condition (see below, section 'M. cucullaris'). This example demonstrates how the choice of extant sample taxa influences the EPB assessment: There is a great danger to generalize observations in a (necessarily small) sample for the whole bracket taxon (in this case, Crocodylia), which may lead to false reconstructions of the plesiomorphic state at the root of the EPB.

A similar risk exists for the second extant taxon that forms the archosaurian EPB, the clade Aves. Because bird forelimbs are highly specialized organs that have been extensively modified during bird evolution, due to their dominating role for locomotion and behavior, one tends to choose the phylogenetically basalmost birds as an adequate sample for all Aves. However, modern palaeognaths are also highly specialized, possibly paedomorphic (de Beer, 1956; Feduccia, 1986) birds that secondarily modified or reduced much of their pectoral girdle and forelimb (Fürbringer, 1886; Steiner, 1949; Cracraft, 1974). With respect to forelimb osteology and myology, these birds actually are of little help to reliantly reconstruct the musculature of basal archosaurs. It is therefore essential to found the EPB assessment on extant sample taxa that resemble a 'generalized plesiomorphic bird'. However, current knowledge does not allow for a secure assessment which bird taxon serves best for this role. Moreover, some bird taxa exhibit a high level of individual myological variation, making it difficult to recognize any phylogenetic signal in their muscular anatomy (McGowan, 1979, 1982, 1986), but these observations cannot be generalized for all Aves (Raikow et al., 1990).

There is still much research to do on the question of constancy of tetrapod muscular anatomy within species or within larger clades, on homologies and phylogenetic history of individual muscles, and on the functionality of muscle groups during locomotion. To gain a comprehensive view on the plesiomorphic myology of archosaurs, the sample size of extant taxa cannot be high enough. For example, Hutchinson (2001a,b, 2002) dissected more than 100 specimens of *Gallus* and additional 85 specimens of various other extant Reptilia for his studies on theropod hindlimb evolution. On the other hand, his paleontological sample was restricted to a small number of specimens that represent major stages in theropod evolution. Due to a focus on a large sample of fossil material, a revision of diapsid forelimb myology based on own dissections would clearly be beyond the temporal and financial scope of the present thesis. Therefore, this chapter follows a different approach: As much published accounts on diapsid forelimb anatomy as possible are reviewed in order to summarize which anatomical details are currently known about the muscular anatomy of the last common ancestor of extant archosaurs, and what is unknown. This should serve as a better fundament for assessing myological evolution of sauropodomorphs or any other extinct archosaur group than adding another individual (and hence probably not representative) observation to the literature.

Archosaurian forelimb myology

In order to get an overview over the complex set of forelimb muscles and their function, the musculature may be subdivided into groups. Different ways of subdivision have been proposed:

In his classic works, Fürbringer (1876, 1888, 1902) recognized the value of homologous innervations in order to homologize individual muscles of the extremities, and grouped the musculature accordingly. Fürbringer (1888) also argued that the connection between nerve and muscle is already fixed at the beginning of ontogenetic development, a suggestion later known as the Fürbringer hypothesis. Gadow and Selenka (1891) followed his approach, and other workers henceforth relied on innervations to identify limb muscles in anatomical studies (e.g., Howell, 1936a,b, 1937). Romer (1922) was the first to express doubts on the reliability of nerve supply as a panacea to questions about muscle homologies. Haines (1935) rejected any requisite connection between muscles and their nerve supply: homologous muscles actually may be innervated by different nerves, due to individual or phylogenetic variation. Therefore, the Fürbringer hypothesis does not necessarily help to homologize crocodilian and avian muscles, and a muscle classification based on innervation patterns would not be suited for the matter discussed in the present work.

A second way of subdividing limb muscles is expressed by the terms ‘extrinsic’ and ‘intrinsic’ musculature. Extrinsic muscles are those that origin from the trunk and act on the limb, while intrinsic muscles are confined to the girdle and limb. Most recently, Meers (2003) adopted this concept and also extended it to distinguish between extrinsic and intrinsic manual flexors and extensors, the former group having its origin on the antebrachium, the latter on the carpus and metacarpus. However, in his works on the embryonic development of lacertilians, Romer (1942, 1944) already showed that such a classification is artificial, because some ‘extrinsic’ muscles (M. latissimus dorsi, M. pectoralis) are clearly derived from the embryonic limb bud muscle mass, while others are modified axial muscles. Furthermore, M. teres major of reptiles is a specialized portion of M. latissimus dorsi that relocated its origin onto the scapular blade; therefore, although plesiomorphically part of an ‘extrinsic’ muscle, it would have to be classified as ‘intrinsic’. For all these logical difficulties, Romer (1942, 1944) abandoned this concept and suggested a classification based on embryonic development.

Romer (1922, 1924) proposed that the pectoral limb of tetrapods is derived from the pectoral fin of fishes, which typically possess only two muscular bodies, a dorsal extensor and a ventral flexor muscle. Therefore, all limb muscles of tetrapods should be derived from one of these muscle masses and may be classified as ‘dorsal’ or ‘ventral’, respectively. His hypothesis was later confirmed by embryological examinations of *Necturus* (Chen, 1935), *Lacerta* (Romer, 1942, 1944), and *Chrysemys* (Walker, 1947). Romer’s hypothesis henceforth served as a standard for limb muscle classification for other scholars (Miner, 1925; Howell, 1936a,b; Walker, 1973; Cong et al., 1998; Meers, 2003; Jasinoski et al., 2006), who sometimes equated dorsal muscles with extensors and ventral muscles with flexors. For instance, Meers (2003) classified the dorsal M. ectepicondylo-ulnaris (‘M. flexor ulnaris’ in his work) as a forearm extensor, although this muscle functionally serves as a flexor, a derived trait. However, many workers, especially ornithologists, refrained from adopting any subdivision of limb muscles, and in anatomical descriptions listed muscles simply in gross proximodistal order (e.g., Vanden Berge and Zweers, 1993). Both concepts are regarded here as not concise enough for a thorough understanding of function and functional change.

Therefore, the muscles of the pectoral girdle and forelimb have been subdivided here into gross functional units that correspond to the mechanical units moved by these muscles. These are, in proximodistal order:

a) muscles that connect the pectoral girdle to the axial skeleton (cingulo-axial muscles),
b) muscles that act on the humerus (humeral muscles),
c) muscles that act on the antebrachium (antebrachial muscles), and
d) muscles that act on the manus, i.e., carpus, metacarpus, and phalanges (manual muscles).

The verb ‘to act’ has to be viewed from an internal, proximodistal frame of reference here, since from a position outside of the animal, it is often not possible to determine ‘fixed’ and ‘moved’ elements during the complex process of locomotion. Byerly (1925) adopted a similar subdivision, albeit with a higher number of less inclusive muscle groups. These functional units are not necessarily ‘natural’ groups in sense of their phylogenetical or embryological derivation, but serve well to understand the functional morphology of the limb, one of the main purposes of the present work.

In the following sections, the morphology and phyletic variation of each forelimb muscle will be shortly described, with special emphasis on potential osteological correlates. Only anatomical and topological aspects will be discussed, since the treatment of functional suppositions about the muscles of modern animals would be beyond the scope of this chapter. Due to the extreme modification of the chelonian pectoral girdle both in form and position, muscles that attach to this structure are hard to compare to those of other tetrapods. Therefore, turtle musculature is taken into full account only in sections III and IV (antebrachial and hand muscles). A simplified cladogramm of the tetrapod groups treated in this chapter is given in figure 3-1.

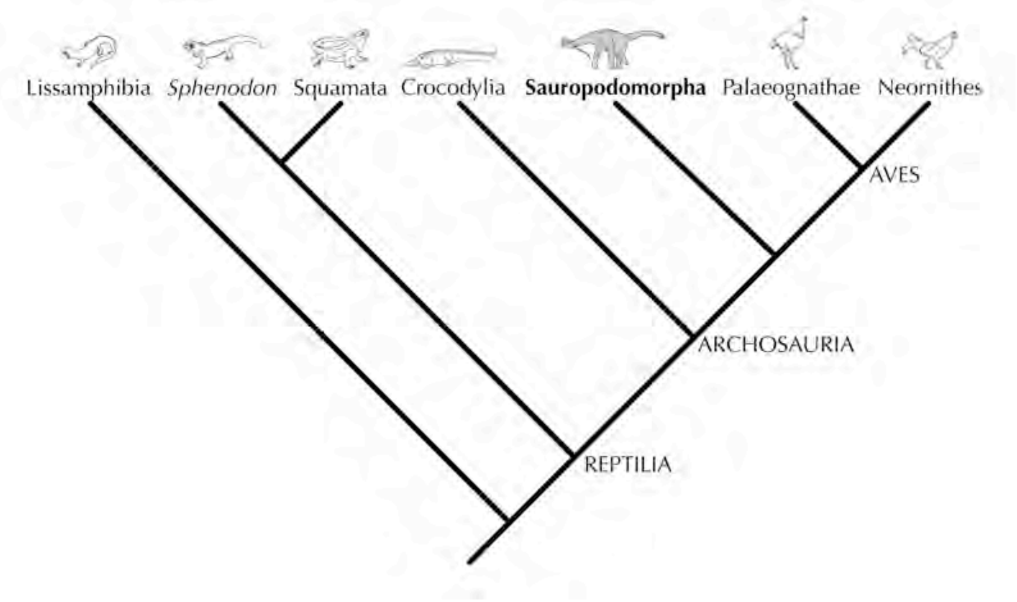

Figure 3-1. Cladogramm of the extant tetrapod groups examined throughout this chapter, and their relationship to sauropodomorphs.

Additionally to the morphological descriptions, nomenclatorial synonyms are also reviewed. The names suggested here follow a concept of ‘best compromise’ between NAA standardization and compatibility to earlier works. As will be shown, some of the NAA concepts also serve well for archosaurs or other diapsids, and should be preferred over misleading terms that exist in the literature on anatomy of non-avian reptiles. A simplified overview of the muscles treated in this chapter is provided in the Appendix of this work.

I. Cingulo-axial muscles

1. M. cucullaris (C).

Synonyms:

- M. trapezius (Haughton, 1866; Mivart, 1867, 1870; de Vis, 1884; Cong et al., 1998; Meers, 2003)
- M. dorso-scapularis (Fürbringer, 1876)
- M. triangularis dorsi primordialis (Ribbing, 1938)

Remarks – Although frequently named 'M. trapezius' in the literature, both the classical works of Fürbringer (1886, 1888, 1900, 1902) and modern ornithological works (e.g., Berger, 1966; Vanden Berge and Zweers, 1993) prefer the term 'M. cucullaris'. The name 'M. trapezius' has its origin in human anatomy, and although both M. trapezius and M. cucullaris are derived from the same primordial muscle mass, they are no strict homologues. Therefore, the term 'M. cucullaris' is most appropriate.

DESCRIPTION – Plesiomorphically, M. cucullaris (figs. 3-2, 3-3) is a thin, sheet-like superficial muscle that has its origin on the occiput and aponeurotically along the cervical dorsal midline, and its insertion on the acromial region of the scapula. In amphibians, the origin of M. cucullaris extends from the exoccipitals back to about the level of the cranial edge of the scapula, and the muscular body is undivided (Miner, 1925; Francis, 1934; Ribbing, 1938). A similar condition is found in *Sphenodon*, however with a slight differentiation into an occipital and a cervical part (Fürbringer, 1876, 1900; Byerly, 1925; Miner, 1925). In squamates as well as in archosaurs, both parts fully differentiate into M. sternocleidomastoideus, which spans along the lateral side of the neck between the occiput and the ventrocranial edge of the sternum, and into M. cucullaris *sensu strictu*. In both groups, the craniocaudal extent of M. cucullaris is variable. In *Iguana*, its origin extends almost from the occiput to the level of the fifth dorsal vertebra (Mivart, 1867), while in *Chamaeleo*, its extent is restricted to one or two dorsal vertebra (Mivart 1870; Fürbringer, 1876, 1900). In crocodilians, the differentiation of the plesiomorphic M. cucullaris is most derived, since not only the areas of origin are separated widely, but also the insertion sites of M. sternoatlanticus (a derivate of M. supracleidomastoideus) and M. cucullaris are neighboring no longer (Fürbringer, 1876, 1886, 1888, 1900, 1902). In amphibians, M. cucullaris inserts along the cranial edge of the scapula down to the contact between scapula and coracoid (Miner, 1925; Ribbing, 1938). The muscle mainly inserts in the acromial area in squamates (Sanders, 1870, 1872; de Vis, 1884; Romer, 1922; Byerly, 1925; Miner, 1925), while its derivate, M. sternocleidomastoideus, inserts laterally at the clavicle, interclavicle, and sternum (Fürbringer, 1876, 1900; Byerly, 1925; Miner, 1925; Ribbing, 1938). Most crocodilians strongly modified the ancestral state by restricting the insertion of M. cucullaris to the cranial edge of the scapula blade, without reaching down to the acromial area, and simultaneously further differentiating M. sternocleidomastoideus into two separate muscles that insert on the cranial edge of the sternum (Fürbringer, 1876; Meers, 2003). These modifications are related to the reduction of the clavicles in crocodilians. However, the insertion site of M. cucullaris is still located immediately caudal to the acromion in *Caiman* (own observations; Jasinoski et al., 2006).

M. cucullaris of birds in a way resembles the ancestral state more than that of crocodilians. The craniocaudal extent of its origin strongly varies, from almost all along the neck in *Rhea* to a small caudal bundle at the base of the neck (Fürbringer, 1876, 1886, 1888, 1900, 1902; Vollmerhaus et al., 1992). In all carinates, M. cucullaris inserts laterally on the furcula, while in ratites, which have lost their clavicles, it inserts on the acromion or dorsal coracoid (Fürbringer, 1876, 1886, 1888, 1902; Gadow and Selenka, 1891). In some bird groups, a specialized slip of M. cucullaris develops that becomes involved in controlling the propatagium (Fürbringer, 1888, 1902; Hudson and Lanzilloti, 1955).

DISCUSSION – Outgroup comparison leaves it unresolved whether the insertion of M. cucullaris along the cranial edge of the scapula blade is a plesiomorphic trait (retained in synapsids and crocodiles) that was reduced in lepidosaurs and lost in birds, or if it is a secondarily derived state of crocodilians, however least expressed in *Caiman*. In the latter case, which is regarded as most parsimonious here, the configuration of M. cucullaris in basal archosaurs should resemble that of *Sphenodon* more than that of *Crocodylus*. A second difficulty is that M. cucullaris usually leaves no osteological correlates (Romer, 1922; own observations). Therefore, reconstructions of this muscle involve a high level of speculation.

2. M. rhomboideus (R).

Synonyms:

M. rhomboides (Fürbringer, 1886, 1888, 1900, 1902)

<u>Remarks</u> – This muscle is consistently named M. rhomboideus in almost all anatomical works, with the exception of the slight difference in writing proposed by Fürbringer. In birds, only M. rhomboideus superficialis is homologous with M. rhomboideus of crocodiles.

DESCRIPTION – M. rhomboideus (fig. 3-3) is restricted to archosaurs and not existent in other diapsids or basal tetrapods. It is regarded as a differentiation of M. serratus profundus, and a convergent development to the homonymous muscles in mammals and anurans (Fürbringer, 1876).

In crocodilians, M. rhomboideus takes its origin from the dorsal fascia, caudal to M. cucullaris and level with the 8th and 9th presacral vertebra (Fürbringer, 1876). A slight differentiation into a cranial and a caudal portion is observable in some taxa, e.g. *Alligator sinensis* (Cong et al., 1998). It consistently inserts onto the medial side of the suprascapular cartilage, commonly in the cranial two thirds (Fürbringer, 1900; Cong et al., 1998; Meers, 2003). Therefore, this muscle has no osteological correlates in crocodilians.

In most birds, two muscles of the name M. rhomboideus exist, M. rhomboideus superficialis and M. rhomboideus profundus. The former is homologous with M. rhomboideus of crocodilians, while the latter is a new derivate of M. serratus profundus (Fürbringer, 1876, 1888, 1902). In carinates, both muscles arise sometimes fleshy, sometimes aponeurotical from the dorsolateral sides of the neural spines, and insert along the dorsal (developmentally cranial) border or dorsomedial rim of the scapular blade. M. rhomboideus superficialis extents its insertion onto the dorsal head of the furcula in some forms (Fisher, 1946; Schreiweis, 1982). The origin and insertion of M. rhomboideus profundus is located somewhat caudal to that of M. rhomboideus superficialis, however both muscles usually overlap for most of their extent (Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Schreiweis, 1982; McGowan, 1986). They are closely associated and sometimes coadunate (Fürbringer, 1888, 1902; McGowan, 1986).

The morphology of Mm. rhomboidei in ratites is variable. In *Rhea* and *Struthio*, M. rhomboideus superficialis is located far cranially and partially coadunate with M. cucullaris (Fürbringer, 1888, 1902). As a consequence, it is completely separate from M. rhomboideus profundus. However, in *Casuarius*, its insertion along the dorsal border of the scapula resembles the condition found in carinates. In *Casuarius* and in *Apteryx*, M. rhomboideus profundus has not fully differentiated as a separate muscle. In both taxa, it is part of M. serratus profundus, and has its origin on the dorsal ribs (Fürbringer, 1888, 1902; McGowan, 1982). However, M. rhomboideus profundus is present in *Rhea, Struthio,* and *Dromaius* (Fürbringer, 1888).

DISCUSSION –Based on the imperfect development in some ratites, Fürbringer (1902) suggested that M. rhomboideus profundus is a novel muscle that is restricted to Aves and only in carinates fully developed. However, since ratites are inadequate for polarizing avian myological characters (see above), it is also possible that M. rhomboideus profundus already was present in dromaeosaurids (Jasinoski et al., 2006), or even earlier in theropod evolution. Given the conjoint insertion dorsomedially on the scapular edge, M. rhomboideus profundus has no osteological correlate that is clearly distinguishable from that of M. rhomboideus superficialis. Therefore, strict phylogenetic inference does not rule out the presence of M. rhomboideus profundus in basal archosaurs, although this is improbable (chapter 4). Nevertheless, the EPB unequivocally implies the presence of a M. rhomboideus (superficialis) in those forms (level I inference), but its extent is a matter of speculation.

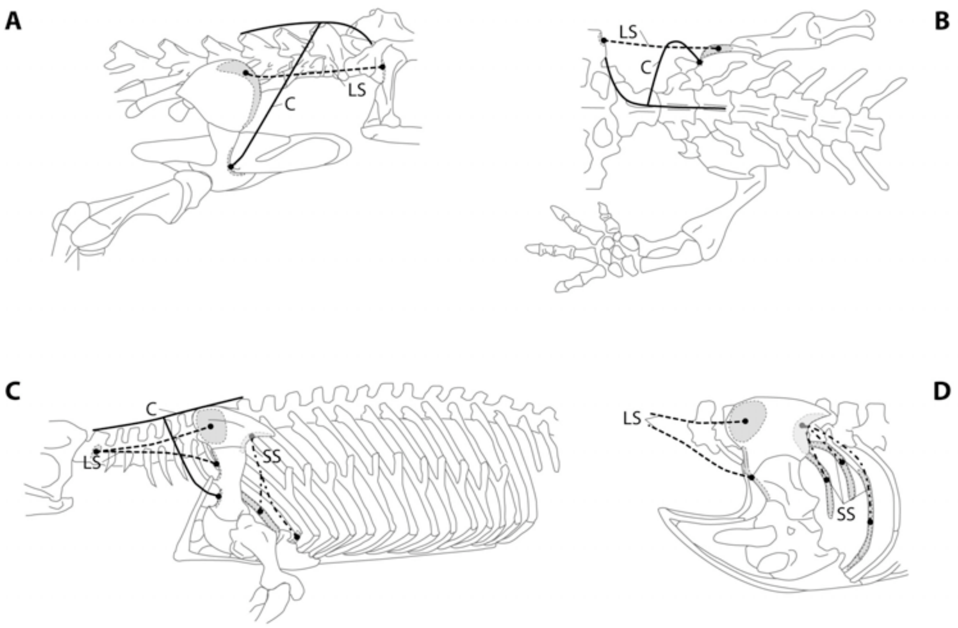

Figure 3-2. Origins, insertions and lines of action of superficial cingulo-axial muscles in urodeles (A, right lateral view; B, dorsal view), *Sphenodon* (C, left lateral view), and *Varanus* (D, left lateral view). Shaded attachment areas and lines of action indicate muscles that lie on the remote side of the respective bony element.

3. M. levator scapulae (LS).

Synonyms:

M. serratus magnus (Haughton, 1866)
M. levator claviculae (Mivart, 1867, 1870)
M. collo-scapularis superficialis (Fürbringer, 1876)
M. levator scapulae superficialis (Fürbringer, 1900; Byerly, 1925; Cong et al., 1998)
M. basi-scapularis (Ribbing, 1938)

Remarks: Fürbringer (1876, 1900) preferred the term M. levator scapulae superficialis, contrasting this muscle to M. levator scapulae et serratus profundus (M. serratus profundus in this work), which also rotates the scapula cranially. However, later workers referred to the superficial muscle simply as M. levator scapulae, a convention followed here.

DESCRIPTION – M. levator scapulae (figs. 3-2, 3-3) is situated on the lateral side of the neck (medial to M. cucullaris) in all tetrapods with the exception of birds and turtles. Probably, it is phylogenetically related to M. cucullaris, as a derivate of the musculature that connected the head and dermal pectoral girdle in lower tetrapods (Romer, 1922). In amphibians, it is still attached to the occiput (Ribbing, 1938). In Reptilia, its origin was transferred to the transverse processes of the first few cervical vertebrae (usually, atlas or axis). In contrast to amphibians, lepidosaurs develop two heads of this muscle (an inferior or ventral head and a superior or dorsal head) that retain a common origin but split caudally towards their insertions (Miner, 1925). In *Sphenodon*, the ventral head inserts medially along the cranial edge of the scapula down to the acromion, while the dorsal head attaches to the craniodorsal part of the lateral side of the suprascapular cartilage (Fürbringer, 1876, 1900; Byerly, 1925; Miner, 1925). This condition has been regarded as specialized by Fürbringer (1900): In other lepidosaurs, such a division of M. levator scapulae into a dorsal and a ventral part is present, but not as pronounced as in *Sphenodon*. The ventral part of the lepidosaurian M. levator scapulae usually attaches to the whole cranial edge of the scapula (sometimes extending onto the lateral side) and also to the lateral side of the dorsal extremity of the clavicle, close to its articulation with the acromion (Mivart, 1867; Sanders, 1870, 1872, 1874; Fürbringer, 1876, 1900; de Vis, 1884; Romer, 1922; Ribbing, 1938).

In crocodilians, the origin of M. levator scapulae extends to the cervical vertebral ribs, but retains an attachment to the cervical transverse processes (Haughton, 1866, Fürbringer, 1876, 1900; Meers, 2003). There is no clear differentiation into a dorsal and a ventral head, although Fürbringer (1876) mentions a slight portioning into a dorsal and a ventral part in some forms. However, Cong et al. (1998) found this muscle to split into a superficial and a deep layer in *Alligator sinensis*.

DISCUSSION – The fleshy origin of this muscle was not found to leave any unambiguous osteological correlates on the cranial cervical transverse processes or ribs that may be distinguished from the areas of attachment of M. serratus profundus. However, the cranial edge of the scapula is slightly thickened at the site of insertion of M. levator scapulae in crocodilians. Moreover, a narrow convex facet may be found cranial to the flattened area of attachment of M. deltoideus scapularis, indicating an extension of M. levator scapulae onto the lateral surface of the scapula.

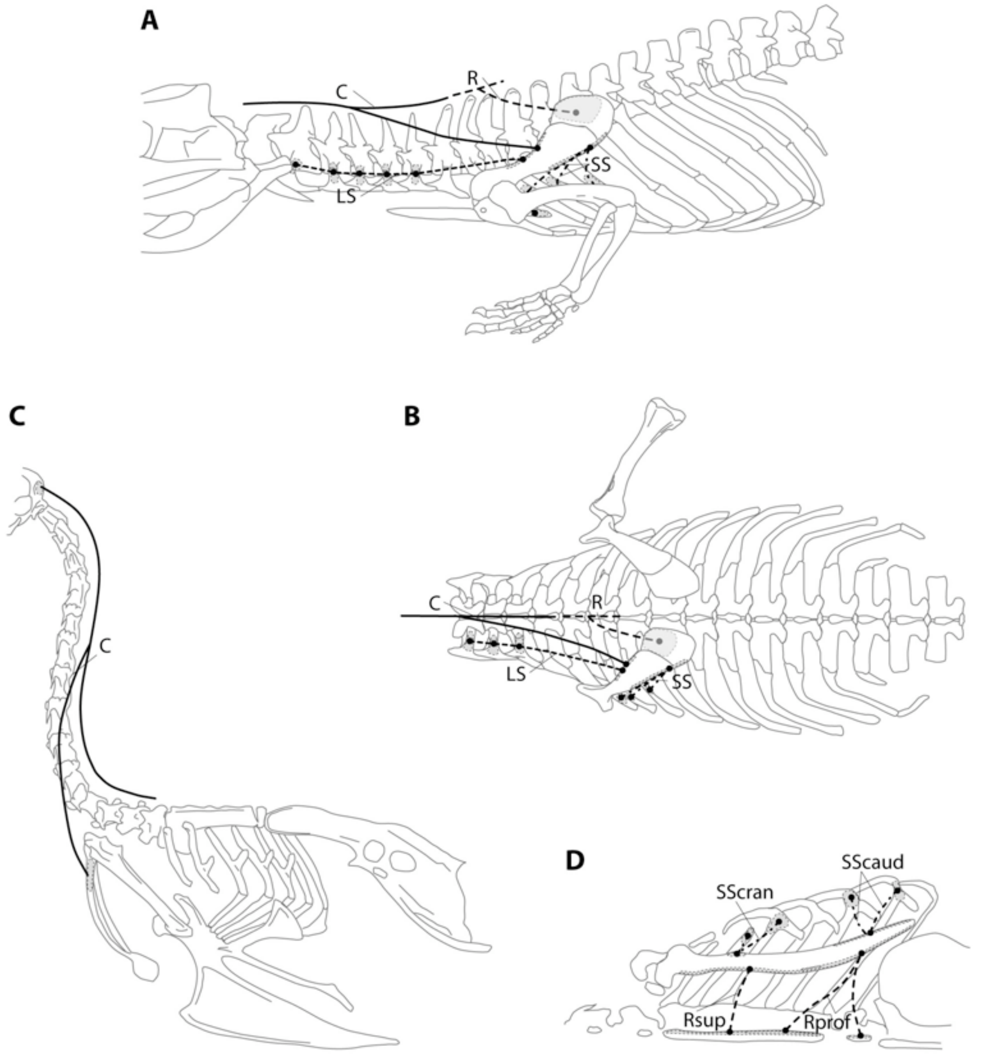

Figure 3-3. Origins, insertions and lines of action of superficial cingulo-axial muscles in *Alligator* (A, left lateral view; B, dorsal view) and *Gallus* (C, left lateral view; D, dorsal view). Shaded attachment areas and lines of action indicate muscles that lie on the remote side of the respective element.

Since M. levator scapulae is lost in birds, it is difficult to reconstruct its morphology in basal archosaurs by phylogenetic inference alone. The development of a dorsal (suprascapular) head in lepidosaurs may be synapomorphic for this group, but this condition may also be plesiomorphic for diapsids and secondarily reduced in crocodiles. However, the latter assumption would be less parsimonious and is therefore not taken into consideration here. Moreover, it can be assumed that M. levator scapulae was lost in birds as a result of the reorientation of the scapula in Maniraptora (Jasinoski et al., 2006). Hence, the muscle probably was still present in basal archosaurs, although the EPB produces equivocal results in this case. The exact extent of the insertion of M. levator scapulae is a matter of speculation, because the associated osteological structures are not easy to identify.

4. M. serratus superficialis (SS).

Synonyms:

M. latissimus dorsi scapulocostalis (Haughton, 1866)
M. serratus magnus (Mivart, 1867, 1870; Ribbing, 1938)
M. thoraci-scapularis superficialis (Fürbringer, 1876)
M. costo-sterno-scapularis (Byerly, 1925)
M. serratus anterior, M. serratus posterior (Fisher, 1946; Fisher and Goodman, 1955; Berger, 1953, 1954, 1955, 1956a–c, 1957, 1960, 1966)
M. serratus ventralis thoracis (Meers, 2003)

Remarks: In reptiles, there are at least two layers of the M. serratus complex, referred to as M. serratus superficialis and M. serratus profundus by most modern workers. Earlier workers subsumed these muscles under 'M. serratus magnus' (Mivart, 1867, 1870; Ribbing, 1938) or simply 'M. serratus' (Sanders, 1870, 1872; de Vis, 1884). Regarding birds, Fisher and Berger (see citations above) subdivided M. serratus superficialis into two or three discrete muscles, namely M. serratus anterior, M. serratus posterior, and M. serratus metapatagialis, additional to M. serratus profundus. However, the NAA recognized the common origin of the three superficial muscles, and standardized their terminology as constituting three different parts of M. serratus superficialis (Vanden Berge and Zweers, 1993).

DESCRIPTION – M. serratus superficialis (figs. 3-2, 3-3) is located on the lateral side of the body just medial and caudal to the scapula, and is covered by M. latissimus dorsi. The muscle connects the scapula to the ribcage, and is characterized by a strong interspecific plasticity in its origin; however, there are commonalities. In *Sphenodon*, the origin of M. serratus superficialis is restricted to the lateral side of the last cervical rib and the first sternal rib. The muscle inserts on the caudoventral edge of the cartilaginous suprascapula and the caudodorsal corner of the bony scapula (Fürbringer, 1900; Miner, 1925). Miner (1925) noted that M. serratus superficialis is not well developed in amphibians, but reduced to a tendinous sheet that connects the posterior edge of the suprascapula to the lateral body wall. In contrast, lepidosaurs usually have this muscle subdivided into two to four slips that have their origin on various ribs in the caudal cervical and cranial thoracic region (including the sternal ribs). These slips insert differently on the suprascapula and sometimes on the caudodorsal edge of the bony scapula (Mivart, 1867, 1870; Sanders, 1870, 1872; Fürbringer, 1876, 1900; de Vis, 1884).

In crocodilians, the threefold origin of M. serratus superficialis is confined to the ventral part of the last cervical rib and to the uncinate processes and adjacent shafts of the first three thoracic ribs (Fürbringer, 1876, 1900). The three slips merge and insert together along the caudal edge of the scapula and suprascapula (Fürbringer, 1876; Cong et al., 1998). The ventral part of this muscle tends to separate the belly of M. subcoracoscapularis into two portions (Fürbringer, 1876, 1900), a development towards the condition seen in birds (see below). M. serratus superficialis is much stronger in crocodilians than in lepidosaurs (Fürbringer, 1876; Ribbing, 1938).

In most birds, M. serratus superficialis has differentiated into three separate muscular bodies called pars cranialis, pars caudalis, and pars metapatagialis, respectively (Gadow and Selenka, 1891; Fürbringer, 1902; Ribbing, 1938; Vanden Berge and Zweers, 1993). Pars cranialis usually arises from the ventral parts of the last cervical and first thoracic ribs, and sometimes also from their uncinate processes. It inserts fleshy, sometimes tendinous on the cranial part of the ventral scapular border and divides M. subcoracoscapularis (M. subscapularis in birds) into two portions (Gadow and Selenka, 1891; Fürbringer, 1902; Fisher, 1946; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; McGowan, 1982, 1986; Schreiweis, 1982; Vanden Berge and Zweers, 1993). If it inserts tendinously, a triangular tubercle on the caudal scapular blade correlates with this muscle (Jasinoski et al., 2006). Pars caudalis takes its origin from various ribs, usually between the second and the sixth thoracic rib, ventral to or directly on the uncinate processes. It inserts on the posterior third of the ventral edge of the scapular blade (Fürbringer, 1902; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; McGowan, 1982, 1986).

The picture is somewhat different in palaeognathous birds. In *Struthio* and *Casuarius*, M. serratus superficialis is undifferentiated. The muscle does not subdivide M. subscapularis, because the tendinous insertion of M. serratus superficialis is situated lateral to the former (Gadow and Selenka, 1891). However, *Rhea* and *Apteryx* show a differentiation of this muscle into a pars cranialis and a pars caudalis, but exhibit no trace of a pars metapatagialis (Fürbringer, 1902; McGowan, 1982). Furthermore, the site of insertion of these muscles has shifted onto the dorsal edge of the scapula in *Rhea* (Fürbringer, 1902).

DISCUSSION – Given the variable condition in ratites, Fürbringer (1902) concluded that the differentiation of M. serratus superficialis into a pars cranialis and a pars caudalis must have occurred at the base of modern birds, and is probably related to the reorientation of the scapula blade. However, this reorientation began earlier in maniraptoran evolution (Gatesy and Baier, 2005), and the primitive condition of M. serratus superficialis in some ratites may in fact be a result of paedomorphosis (see above, 'Variation and the choice of extant sample taxa'). Nevertheless, more basal theropods show a plesiomorphic orientation of the pectoral girdle (Carpenter, 2002). Therefore, a crocodilian-like, undivided insertion along the entire caudal margin of the scapula probably was present in all archosaurs plesiomorphically. However, the exact extent of this insertion is hard to delimit, since no unambiguous osteological correlates are present in the extant bracket taxa.

5. M. serratus profundus (SP).

Synonyms:

M. serratus magnus (Mivart, 1867, 1870; Ribbing, 1938)
M. serratus anterior (Sanders, 1870, 1872; Romer, 1922)
M. collo-thoraci-scapularis profundus (Fürbringer, 1876)
M. levator scapulae et serratus profundus (Fürbringer, 1900)
M. rhomboideus (Rabl, 1916)
M. serratus anticus (Byerly, 1925)
M. serratus profundus ventralis (Cong et al., 1998)
M. serratus ventralis cervicis (Meers, 2003)

<u>Remarks</u>: Most authors recognized M. serratus profundus as a part of the Mm. serrati complex, but several synonyms have been proposed (see list above). However, the NAA uses the term M. serratus profundus (Vanden Berge and Zweers, 1993), a useful standardization that is easily applicable to the anatomical conditions in lower diapsids. Few authors (e.g., Meckel, 1828; Rabl, 1916) have suggested that parts of this muscle may be homologous to M. rhomboideus of archosaurs (and mammals, rendering this muscle an amniote synapomorphy), a hypothesis rejected by Fürbringer (1876, 1900).

DESCRIPTION – Like M. serratus superficialis, M. serratus profundus (figs. 3-4, 3-5) is located on the lateral side of the body. It is covered by the former muscle, by the scapular blade, and by M. latissimus dorsi. With the exception of mammals and carinate birds, it is divided into a superficial and a deep layer in most other tetrapods. The deep layer usually has a wider origin than the superficial layer (Ribbing, 1938; Fürbringer, 1876, 1900, 1902; Gadow and Selenka, 1891). In amphibians, M. serratus profundus arises from the ends of the two middle cervical ribs (Miner, 1925), or from the transverse processes of the last two cervical vertebrae (Ribbing, 1938), and inserts on the medial surface of the suprascapular cartilage. The area of insertion is conservative in non-avian diapsids, but the points of origin on the axial skeleton are highly variable. The origin of M. serratus profundus usually comprises the ventral parts of all six cervical ribs in *Sphenodon*, and its deep layer inserts along the dorsomedial border of the suprascapula (Fürbringer, 1900; Byerly, 1925; Miner, 1925). In other lepidosaurs, this muscle variably arises from two to six cervical ribs (Fürbringer, 1876, 1900; Mivart, 1867; Sanders, 1870, 1872; Rabl, 1916; Ribbing, 1938), but usually not from the transverse processes.

In archosaurs, the muscle retains the origin from the transverse processes. In *Alligator,* the attachment of M. serratus profundus comprises the ribs and transverse processes of the fifth (or sixth) to tenth cervical vertebra (Fürbringer, 1900). In other crocodilians, this origin may extent caudally to the dorsal edge of the uncinate process of the second thoracic rib (Fürbringer, 1876, 1900). Like in lepidosaurs, M. serratus profundus inserts on the medial side of the suprascapular cartilage, but sometimes extends ventrally onto the dorsal edge of the bony scapula, where it is partially associated with a rugose surface texture (Jasinoski et al., 2006; own observations).

The superficial layer of M. serratus profundus tends to fuse with M. serratus superficialis pars posterior in all birds but *Struthio* and *Casuarius*, where the primitive reptilian condition is retained (Fürbringer, 1902). Moreover, with the exception of *Apteryx* and *Casuarius*, a new derivate of M. serratus profundus developed, M. rhomboideus profundus (Fürbringer, 1886; see above, 'M. rhomboideus'). The remaining main portion of M. serratus profundus is highly variable. It has its origin on two to six ribs in the caudal cervical and cranial thoracic region. The points of attachment locate sometimes ventrally, sometimes proximally, and in the latter case also include the adjacent transverse processes. In most cases, the origin is situated on the last two cervical ribs plus the first and sometimes second thoracic rib. The muscle also extends cranially in some forms, which has been explained by a shift of the pectoral girdle relatively backwards along the vertebral column (Fürbringer, 1902). M. serratus profundus generally inserts on the medial surface of the caudal part of the scapular blade, but the outline and exact position of the area of attachment is variable (Gadow and Selenka, 1891; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; Schreiweis, 1982).

DISCUSSION – The usually fleshy attachments of M. serratus profundus do not have any unambiguous osteological correlates on the ribs, transverse processes, or scapula (with the exception in crocodilians mentioned above). However, the general area of origin and insertion is relatively constant in all diapsids. Given its morphology in both crocodilians and birds, it is justified to infer that in basal archosaurs M. serratus profundus took its origin from the transverse processes and ribs of the last cervicals and first dorsals, and consisted of two layers (level I inferences). Reconstructing its point of insertion in basal archosaurs involves more speculation, since the cartilaginous suprascapula is lost in birds, but was probably still present in non-maniraptoran dinosaurs (level II inference).

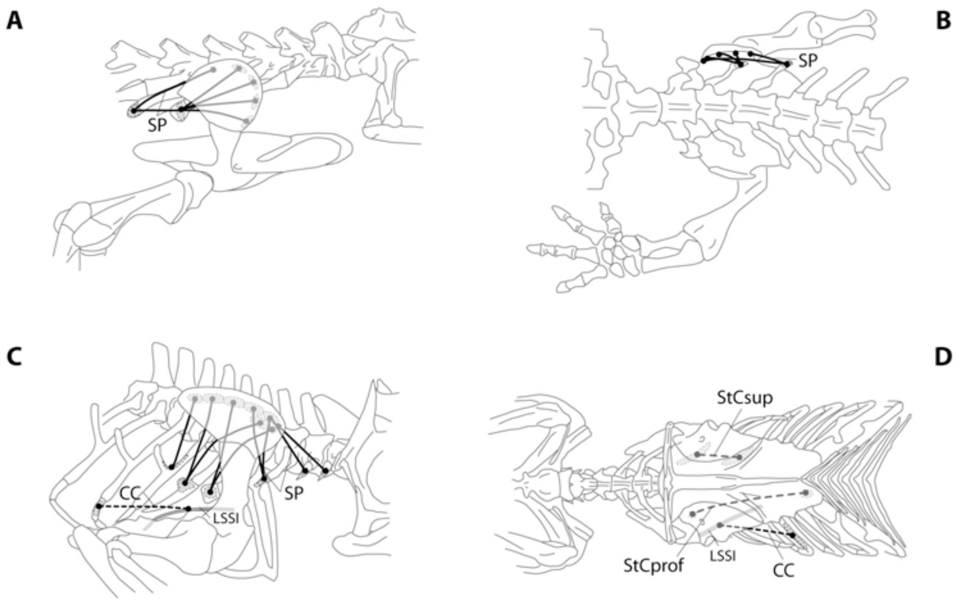

Figure 3-4. Deep cingulo-axial muscles of urodeles (A, right lateral view; B, dorsal view) and lepidosaurs, here *Sphenodon* (C, right lateral view; D, ventral view). Shaded attachment areas and lines of action indicate muscles that lie on the remote side of the respective bony element.

6. M. costocoracoideus (CC).

Synonyms:

M. pectoralis secundus (Haughton, 1866)
M. sternocosto-scapularis (Fürbringer, 1876, 1900)
M. costosterno-coracoideus (Miner, 1925; Dilkes, 2000)
M. sternocoracoideus internus (Ribbing, 1938)

Remarks: The term M. costocoracoideus is fully appropriate only for crocodilians, although many authors also use this name for a certain muscle in lepidosaurs (see below). It has not been shown beyond doubt that the crocodilian M. costocoracoideus is homologous to M. sternocoracoideus in birds (*contra* Jasinoski et al., 2006). Therefore, both muscles are treated separately here.

DESCRIPTION – M. costocoracoideus (figs. 3- 4, 3-5) and M. sternocoracoideus are closely related. Muscles of these names exist in parallel in lepidosaurs, but archosaurs only have one muscle left, a M. costocoracoideus in crocodilians and a

M. sternocoracoideus in birds. However, the homologies of these muscles are unclear (see Discussion).

In *Sphenodon*, there are three muscles on the ventral side of the body that connect the axial skeleton to the pectoral girdle: M. sternocoracoideus superficialis, M. sternocoracoideus profundus, and M. costocoracoideus. Miner (1925) interpreted all of these muscles as derivates of M. sternohyoideus of amphibians, the cranial-most part of the ventral axial musculature. In *Sphenodon* and other lepidosaurs, a small M. costocoracoideus arises from the cranial edge of the first sternal rib (Mivart, 1867; Fürbringer, 1876, 1900; de Vis, 1884; Rabl, 1916; Miner, 1925). The muscle inserts into the prominent Ligamentum sternoscapulare internum, which spans between the medial side of the scapula (dorsocranial to the glenoid) and the dorsolateral side of the sternum. A branch of this ligament inserts onto the coracoid, directly medial to the glenoid. Since the inserting M. costocoracoideus is oriented towards the scapula in lepidosaurs, the main action of this muscle is to rotate the scapula backwards, while the effect on the coracoid is minor.

In crocodilians, M. costocoracoideus is not associated with the Ligamentum sternoscapulare internum. Instead, the large muscle is subdivided into a superficial and a deep head that arise from the cranial edges of the last cervical rib and the first sternal rib, respectively, and jointly insert onto the caudal and medial sides of the coracoid (Haughton, 1866; Fürbringer, 1876, 1900; Cong et al., 1998; Meers, 2003). There is no osteological correlate of M. costocoracoideus in crocodilians. However, the potentially homologous M. sternocoracoideus of birds is correlated with a marked depression on the coracoid (see ‘M. sternocoracoideus’).

DISCUSSION – None of the aforementioned authors make a clear statement if the crocodilian M. costocoracoideus is homologous to the Mm. sternocoracoidei or to M. costocoracoideus of lepidosaurs. Moreover, it is not clear if M. sternocoracoideus of birds is a homologue of the crocodilian M. costocoracoideus or of the lepidosaurian muscles of the same name (see below, ‘M. sternocoracoideus’). Jasinoski et al. (2006) assumed the former to be the case, based on similar attachment sites and patterns of innervation. However, since all these muscles are derived from a common primordial muscle, there is currently no way to test this assumption: the conditions in all three clades (Lepidosauria, Crocodylia, Aves) may constitute autapomorphic specializations. Therefore, phylogenetic inference only allows to state that in basal archosaurs one or more muscles existed that arose from the medial side of the sternum and/or the cranial edge of the first sternal rib, and inserted caudally and medially on the coracoid (see below, 'M. sternocoracoideus').

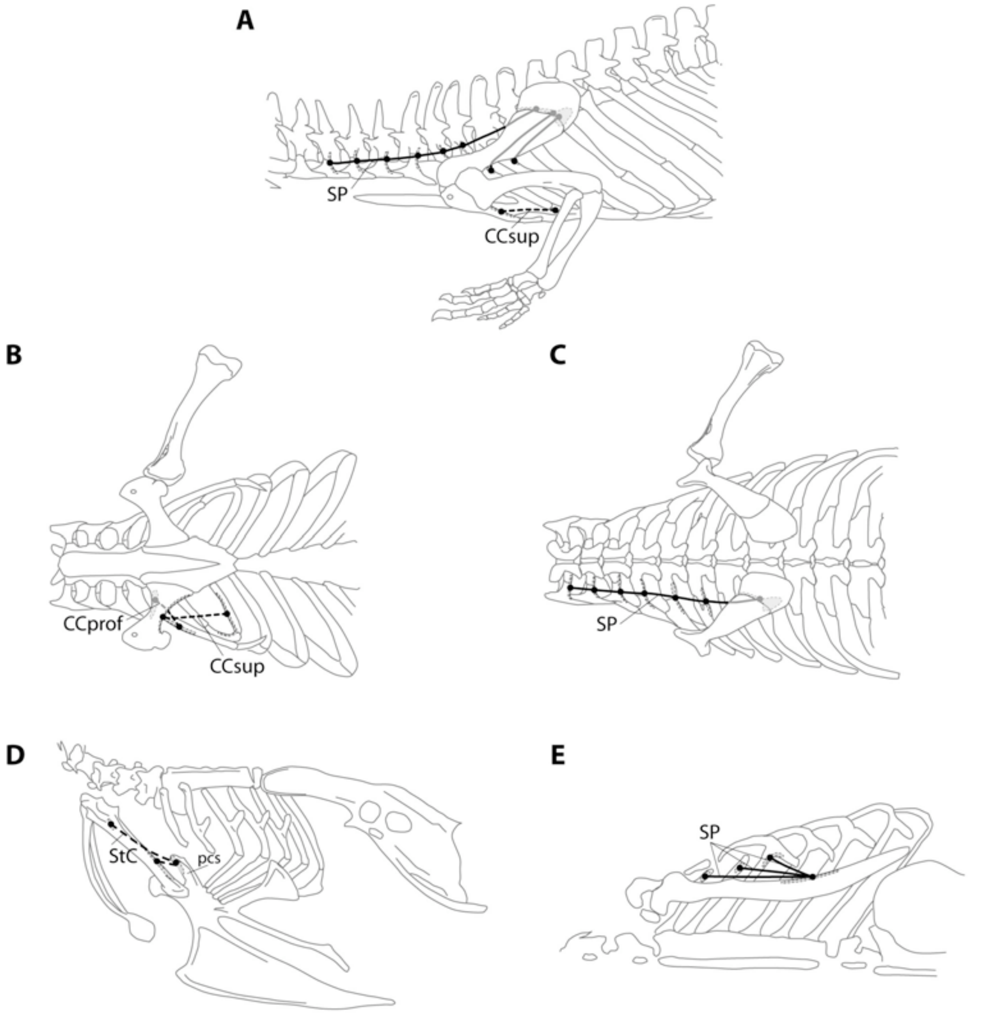

Figure 3-5. Deep cingulo-axial muscles of *Alligator* (A, lateral view; B, ventral view; C, dorsal view) and *Gallus* (D, lateral view; E, dorsal view). Shaded attachment areas and lines of action indicate muscles that lie on the inside of the respective bony element.

7. M. sternocoracoideus (StC).

Synonyms:

M. sterno-coracoidalis (Sanders, 1870, 1872, 1874)

<u>Remarks</u>: see 'M. costocoracoideus' above.

DESCRIPTION – M. sternocoracoideus (figs. 3-4, 3-5) is found in birds and lepidosaurs, but not in crocodilians. The lepidosaurian M. sternocoracoideus arises with two heads (M. sternocoracoideus superficialis and M. sternocoracoideus profundus) from the dorsal (internal) side of the sternum. In dorsal view, the external M. sternocoracoideus superficialis is covered by the internal M. sternocoracoideus profundus. In *Sphenodon* and squamates, the M. sternocoracoideus superficialis takes its origin from the craniolateral side of the sternum, close to the coracoidal articulation, while the latter arises from the caudal half of the sternum. The two heads may extend their origin onto the bases of the sternal ribs, and are partially separated from each other by the Ligamentum sternoscapulare internum. Both muscles join and insert on the medial side of the coracoid. The insertion of M. sternocoracoideus superficialis is fleshy, while that of M. sternocoracoideus profundus is often tendinous and located cranial to the former (Mivart, 1867; Sanders, 1872, 1874; Fürbringer, 1876, 1900; Byerly, 1925; Miner, 1925; Ribbing, 1938).

In birds, M. sternocoracoideus is sometimes undivided (e.g., in *Struthio* and *Rhea*), and sometimes separated into a superficial and a deep layer. The muscle arises primarily from the medial and often also from the lateral side of the Processus craniolateralis sterni (sternocoracoidal process). Like in lepidosaurs, this origin may extend onto the sternal ribs in carinates, but this is not observed in ratites. If present, the superficial part inserts on the lateral process of the coracoid (close to the sternal articulation), while the deep part inserts into a characteristic triangular depression (Impressio m. sternocoracoidei) on the dorsomedial side of the coracoid near its sternal base (Gadow and Selenka, 1891; Fürbringer, 1902; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; McGowan, 1982, 1986; Schreiweis, 1982). The Impressio m. sternocoracoidei may cover almost half of the internal side of the coracoid in some forms, e.g. in Galliformes (Hudson and Lanzilloti, 1964).

DISCUSSION – Fürbringer (1886, 1888, 1902) homologizes the M. sternocoracoideus complex of birds with that of lepidosaurs, but assumes that the superficial and deep layers are not homologous. Instead, he suggests that the muscle observed in birds is a derivate of M. sternocoracoideus superficialis of lepidosaurs (Fürbringer, 1902), probably based on similar points of origin and insertion close to the sternocoracoidal joint. To the author's knowledge, no workers except Jasinoski et al. (2006) suggest that M. sternocoracoideus of birds may be fully homologous to M. costocoracoideus of crocodiles. If Fürbringer's (1902) hypothesis is correct, then both a M. sternocoracoideus and a M. costocoracoideus must have existed in basal archosaurs. The former muscle would then have been reduced on the crurotarsan line, the latter on the ornithodiran line. Both reductions are probably related to the strong modifications of the coracoids in crocodilians and birds. M. sternocoracoideus shows unambiguous osteological correlates in birds (origin: Processus craniolateralis sterni, insertion: Impressio m. sternocoracoidei), but no clear homologues of these structures are present in crocodilians or basal archosaurs. In summary, since the homologies of the ventral cingulo-axial muscles are not fully resolved, there is room for speculation regarding their presence in basal archosaurs. Some osteological structures of fossil sauropodomorphs may indeed be interpreted as evidence for the presence of both M. sternocoracoideus and M. costocoracoideus (chapters 4-9).

II. Humeral muscles.

8. M. deltoideus scapularis (DS).

Synonyms:

M. infraspinatus (Haughton, 1866; Sanders, 1870, 1872, 1874)

M. suprascapularis anterior (Mivart, 1870)

M. dorsalis scapulae (Fürbringer, 1876, 1900; Byerly, 1925; Francis, 1934; Ribbing, 1938; Cong et al., 1998; Walthall and Ashley-Ross, 2006)

Remarks: Although early authors tried to homologize this muscle with the mammalian M. infraspinatus, its affiliation with the Mm. deltoidei system has been demonstrated by comparative works of Fürbringer (1876, 1886, 1900) and embryological analyses (Romer, 1944). Although most classic authors prefer the term 'M. dorsalis scapulae' over 'M. deltoideus scapularis', recent works on dinosaurian shoulder anatomy use the latter name (Nicholls and Russell, 1985; Dilkes, 2000; Jasinoski et al., 2006), a convention that is accepted here. It is not clear whether the avian M. deltoideus major is homologous to M. deltoideus scapularis of other diapsids, as assumed by Nicholls and Russell (1985) and Jasinoski et al. (2006). Fürbringer (1888, 1902) supposes that M. deltoideus scapularis is completely lost in birds, rendering all avian deltoid muscles derivates of M. deltoideus clavicularis. Therefore, these muscles will be discussed in the following paragraph ('M. deltoideus clavicularis').

DESCRIPTION – M. deltoideus scapularis (figs. 3-6, 3-7) is present early in tetrapod evolution, and remains relatively conservative. In amphibians, it arises laterally from the center of the suprascapular cartilage and inserts dorsolaterally on the deltopectoral crest (Fürbringer, 1876; Miner, 1925; Francis, 1934; Walthall and Ashley-Ross, 2006). The condition found in *Sphenodon* is similar to that of amphibians, since the main portion of the origin of M. deltoideus scapularis is still situated on the suprascapula (Fürbringer, 1900; Miner, 1925). In other lepidosaurs, the muscle shows variation in its extent and grade of association with M. deltoideus clavicularis. The caudal side of the clavicle and the dorsal region of the acromion serve as additional areas of origin. In some forms, it is hard to separate M. deltoideus scapularis from M. deltoideus clavicularis, especially near their insertion (Mivart, 1867; Sanders, 1874; Fürbringer, 1876, 1900; de Vis, 1884; Rabl, 1916; Ribbing, 1938). However, other squamates (e.g., chamaeleonids) show a complete separation of these muscles, in both origin and insertion. In these forms, M. deltoideus clavicularis keeps its fleshy insertion on the external side of the deltopectoral crest (see below, 'M. deltoideus clavicularis'), while M. deltoideus scapularis tendinously attaches somewhat more dorsoproximal on the humerus (Mivart, 1870; Sanders, 1870, 1872; Fürbringer, 1876, 1900). This condition is also found in *Sphenodon* (Byerly, 1925; Miner, 1925).

Crocodilians have a smaller M. deltoideus scapularis that shows no attachment to the acromial region. However, the muscle is often bipennate and therefore relatively forceful (Fürbringer, 1876; Meers, 2003). It arises from the cranial or dorsocranial part of the lateral side of the scapular blade, but does not extend much onto the suprascapula. Like in *Sphenodon* and many squamates, M. deltoideus scapularis inserts by a tendon on the dorsocranial side of the humerus close to the humeral head, proximal to the insertion of M. deltoideus clavicularis (Haughton, 1866; Fürbringer, 1876, 1900; Cong et al., 1998; Meers, 2003; Jasinoski et al., 2006). The origin of M. deltoideus scapularis correlates to a flattened area on the dorsolateral scapular blade, but is hard to delimit. Its tendinous insertion on the humerus may be indicated by a low tubercle.

DISCUSSION – Given the condition found in *Sphenodon*, many squamates, and crocodilians, separate insertions of M. deltoideus scapularis and M. deltoideus clavicularis are plesiomorphic for diapsids, and therefore were present in basal archosaurs, too. However, since birds seemingly have completely lost this muscle (Fürbringer, 1888, 1902), the EPB allows only for a level II inference here. In extinct forms, a flattened area craniodorsolaterally on the scapular blade, and a tubercle proximal to the deltopectoral crest may be interpreted as traces of M. deltoideus scapularis, but this conclusion involves some speculation.

9. M. deltoideus clavicularis (DC).

Synonyms:

- M. cleido-humeralis, M. coraco-humeralis anterior et sterno-humeralis posterior (Fürbringer, 1876)
- M. cleido-humeralis (Byerly, 1925)
- M. procoracohumeralis (Miner, 1925; Walthall and Ashley-Ross, 2006)
- M. acromialis (Ribbing, 1938)
- M. deltoideus major, M. deltoideus minor, M. deltoideus propatagialis (ornithological literature)

Remarks: Many authors referred to this muscle simply as M. deltoideus, but the use of the term 'M. deltoideus scapularis' instead of 'M. dorsalis scapulae' throughout this work makes the epithet 'clavicularis' necessary. As has been noted under paragraph 'M. deltoideus scapularis' above, it is assumed that all deltoid muscles of birds are derivates of M. deltoideus clavicularis (see Discussion below). Therefore, all these muscles are discussed in this paragraph.

DESCRIPTION – M. deltoideus clavicularis (figs. 3-6, 3-7) shows much variation, and it is not always easy to homologize the various derivates of the deltoideus complex of extant tetrapods. In caudate amphibians, its probable homologue, M. procoracohumeralis superficialis, arises from the craniolateral face of the coracoid and inserts proximally on the cranial side of the deltopectoral crest of the humerus (Miner, 1925; Francis, 1934; Walthall and Ashley-Ross, 2006). In anurans, the muscle takes origin from the clavicle and interclavicle and inserts in a wide area along the humeral shaft (Fürbringer, 1876; Ribbing, 1938).

The site of insertion of M. deltoideus clavicularis is relatively conservative in sauropsids, whereas its origin is subject to major variances. In all sauropsids, the muscle is located superficially in the cranial region of the shoulder. In *Sphenodon*, the origin is situated on the ventral part of the lateral side of the clavicle and on the cranial part of the interclavicle, including the caudal margin of the transverse processes of that element. M. deltoideus clavicularis inserts dorsocranially on the deltopectoral crest (Fürbringer, 1900; Byerly, 1925; Miner, 1925).

An origin from the ventral clavicle and its caudal margin is retained in most squamates (Mivart, 1867; Sanders, 1870, 1872; Fürbringer, 1876, 1900; de Vis, 1884). An occasional origin from the interclavicle has also been reported (Sanders, 1874; Rabl, 1916; Ribbing, 1938). Fürbringer (1876, 1900) observed a positive correlation between the width of the ventral part of the clavicle and the size of M. deltoideus clavicularis. Fibers that arise from the cranial part of the clavicle wrap around its cranial border and form the deep part of this muscle (Fürbringer, 1876). As in *Sphenodon*, the fleshy insertion of M. deltoideus clavicularis is located on the cranial face of the deltopectoral crest, distal to M. deltoideus scapularis (Mivart, 1867; Sanders, 1870, 1872, 1874; Fürbringer, 1876, 1900; de Vis, 1884; Rabl, 1916).

It is self-evident that in sauropsids with reduced clavicles the origin of M. deltoideus clavicularis is modified. In chameleons, the origin of this muscle has shifted onto the craniolateral edge of the coracoid and the adjacent sternum (Mivart, 1870; Fürbringer, 1876, 1900), while in turtles, the muscle is highly variable and arises from the crista deltoidea on the internal side of the plastron (Ribbing, 1938; Walker, 1973). The relatively large M. deltoideus clavicularis of crocodilians takes its origin from the acromial region and along the cranial edge of the scapula. The muscle inserts fleshy on the cranial side of the deltopectoral crest (Haughton, 1866; Fürbringer, 1876; Nicholls and Russell, 1985; Cong et al., 1998; Meers, 2003).

The deltoid muscles of birds are highly modified in comparison to those of other sauropsids. Three derivates of the deltoid system are recognized, M. deltoideus major, M. deltoideus minor, and M. deltoideus propatagialis (= M. tensor propatagialis). The latter muscle, a derivate of M. deltoideus major only found in carinates, controls the tension of the propatagial skin. Therefore, it is not relevant for the subject of this thesis and will not be further discussed.

M. deltoideus major is present in all birds, and is usually subdivided into two heads (Vanden Berge and Zweers, 1993). Together with M. pectoralis and M. supracoracoideus, it belongs to the most important flight muscles. M. deltoideus major arises from the acromion process or from a larger area on the lateral side of the scapular head, as well as from the dorsal part of the lateral side of the furcula (Fürbringer, 1888, 1902; Fisher, 1946; McGowan, 1986; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; Vollmerhaus et al., 1992). In some forms, it also has a tendinous, sometimes fleshy connection to the dorsal edge of the scapula (Fürbringer, 1888, 1902; Hudson and Lanzilloti, 1955). In ratites, the origin of M. deltoideus major is restricted to the scapular acromion process, as a consequence of the reduction of the clavicles (Fürbringer, 1902; Berger, 1966; McGowan, 1982). In all birds, the muscle inserts fleshy on the deltopectoral crest, and additionally on the dorsal or caudodorsal side of the humeral shaft in many forms (Fürbringer, 1888, 1902; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; McGowan, 1982, 1986; Schreiweis, 1982).

M. deltoideus minor, the most deep-seated of all shoulder muscles, is lost in most ratites, or fully merged with M. deltoideus major in *Struthio* (Fürbringer, 1888, 1902; Gadow and Selenka, 1891, McGowan, 1982). In neognaths, the muscle lies caudal and parallel to M. deltoideus major, and arises from the bones and ligaments around the triosseal foramen (Fürbringer, 1888, 1902; Ribbing, 1938; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; McGowan, 1986). Thus, its origin is located on the proximal clavicle and the acromion process, and in contrast to M. deltoideus major also on the coracoid. The latter origin may expand along the coracoid ventrally to the sternum in some groups, including penguins and *Gallus* (Fürbringer, 1902; Schreiweis, 1982; Vollmerhaus et al., 1992). M. deltoideus minor inserts close to M. deltoideus major on the proximal part of the cranial face of the deltopectoral crest, between the dorsal tubercle of the humerus and the caudal ridge (margo caudalis) of the shaft (Fürbringer, 1888, 1902; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964).

DISCUSSION – Considering the distribution among tetrapods, an origin from the ventral clavicle and the interclavicle seems to represent the plesiomorphic condition of M. deltoideus clavicularis. However, in extant archosaurs all deltoid muscles are located dorsally in the shoulder region. Therefore, Fürbringer (1876) doubts that the crocodilian M. deltoideus clavicularis is fully homologous to its namesake in lepidosaurs. Instead, it may have developed from a fusion of parts of both M. deltoideus scapularis and M. deltoideus clavicularis (Fürbringer, 1876).

The situation in birds is even more complicated. Fürbringer (1888, 1902) assumes M. deltoideus major to be a homologue of the crocodilian M. deltoideus clavicularis. However, some authors (especially those who reconstructed musculature in dinosaurs) have homologized the avian M. deltoideus major with M. deltoideus scapularis of other sauropsids (Ribbing, 1938; Nicholls and Russell, 1985; Dilkes, 2000; Jasinoski et al. 2006), rendering the avian M. deltoideus propatagialis the only derivate of the crocodilian M. deltoideus clavicularis, and the avian M. deltoideus minor a new muscle without homologues in other tetrapods. In contrast, based on the sites of origin and patterns of innervation of avian deltoid muscles, Fürbringer (1888, 1902) states that it is more plausible that M. deltoideus scapularis has been completely lost in birds (probably as a consequence to the reorientation of the scapula). He also assumes that both M. deltoideus minor and M. deltoideus propatagialis are derivates of a primordial M. deltoideus major (and therefore of a muscle related to the crocodilian M. deltoideus clavicularis). Because Fürbringer (1888, 1902) is the only author among those listed above who justified his assumptions with arguments, his model is favored in the present thesis.

Due to these unsolved questions of homology, it is difficult to reconstruct the cranial deltoid musculature of basal archosaurs with certainty. Strict phylogenetic inference implies that a clavicular deltoid muscle (that gave rise to the crocodilian M. deltoideus clavicularis on the one hand and to the avian Mm. deltoidei major et minor on the other) was located dorsally and arose from the acromion and clavicle. However, under consideration of the condition seen in other sauropsids and the presence of both an interclavicle and clavicles with robust ventral ends in basal archosaurs (chapter 4), it is also possible that the deltoid musculature of forms like *Euparkeria* still resembled the lepidosaurian condition more than that of birds and crocodiles (which both possess highly modified pectoral girdles). Nevertheless, given the loss of the interclavicle and reduction of the clavicle in ornithodirans (e.g., Benton, 2004), it is at least probable that basal dinosaurs had a dorsally placed M. deltoideus clavicularis (not necessarily a strict homologue of its crocodilian namesake), but it is impossible to say if this muscle was already differentiated into a M. deltoideus major and a M. deltoideus minor. The EPB implies that this muscle arose at least from the dorsal part of the clavicle and the acromial region of the scapula, and inserted on the (developmentally) cranial side of the deltopectoral crest. To decide if its origin extended onto the cranial edge of the scapula blade as in crocodilians is speculative (level II inference).

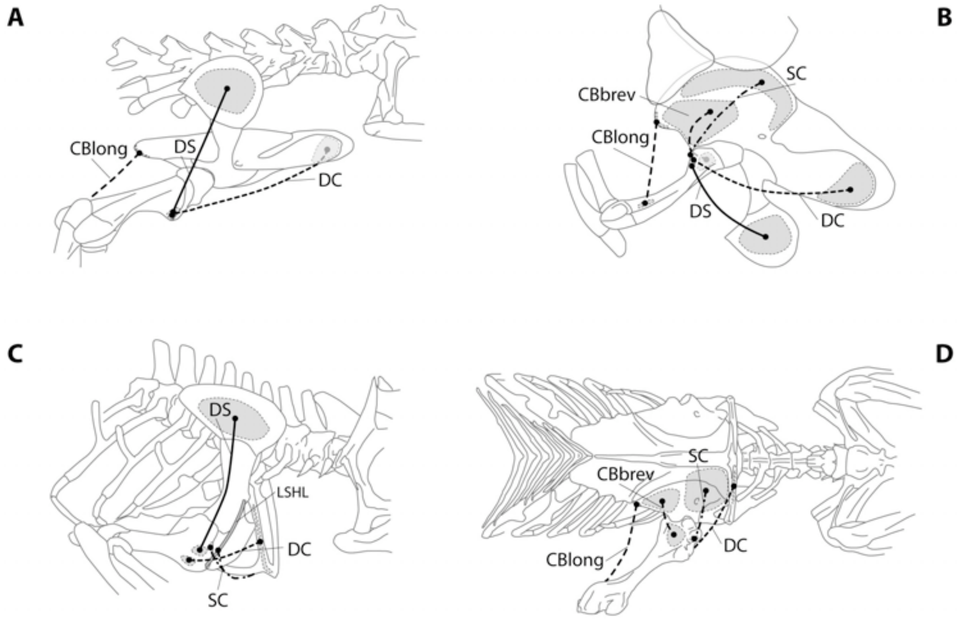

Figure 3-6. Superficial humeral muscles arising from the pectoral girdle in urodeles (A, lateral view; B, ventral view) and *Sphenodon* (C, lateral view; D, ventral view). Shaded attachment areas and lines of action indicate muscles that lie on the remote side of the respective bony element.

10. M. coracobrachialis (CB).

Remarks: There are no synonyms for M. coracobrachialis in the literature. However, there is some variation in the naming of the individual heads of this muscle. Most authors use the terms M. coracobrachialis brevis and M. coracobrachialis longus for the two heads present in non-avian reptiles and amphibians. The NAA uses the terms M. coracobrachialis cranialis and M. coracobrachialis caudalis, but the latter muscle actually is derived from the M. subcoracoscapularis system (Sullivan, 1962) and will therefore be discussed under ‘M. subcoracoscapularis’ below.

DESCRIPTION – The relatively conservative M. coracobrachialis (figs. 3-6, 3-7) is plesiomorphically subdivided into two heads. The short head, M. coracobrachialis brevis, has its fleshy origin on the caudal half of the outside (i.e., ventrolateral surface) of the coracoid in caudate amphibians (Miner, 1925; Francis, 1934; Walthall and Ashley-Ross, 2006) and virtually all lepidosaurs. In some forms, the origin extends cranially to cover almost the complete ventrolateral surface of the coracoid (Mivart, 1867, 1870; Sanders, 1874; Rabl, 1916). The muscle inserts onto the ventral side of the humerus between the deltopectoral crest and the medial tuberosity, usually covering the proximal half or two thirds of the shaft. The insertion often correlates to a depression. The other head, M. coracobrachialis longus, arises caudally to M. coracobrachialis brevis from a small area on the lateral face of the caudal angle (in caudate amphibians, from the caudal edge) of the coracoid. In some forms, the origin may extend onto the medial side of the coracoid, and onto the Ligamentum sternoscapulare internum (see ‘M. costocoracoideus’ above). M. coracobrachialis longus runs parallel to the medial side of the humerus and inserts on or slightly proximal to the humeral entepicondyle (Mivart, 1867, 1870; Sanders, 1870, 1872, 1874; Fürbringer, 1876, 1900; de Vis, 1884; Rabl, 1916; Romer, 1922; Miner, 1925).

Crocodilians have completely lost the long head of M. coracobrachialis. The remaining M. coracobrachialis brevis arises from almost the entire external surface of the coracoid, with the exception of the cranial and medial edges (Fürbringer, 1876; Meers, 2003; own observation). Like in more basal tetrapods, it inserts ventrally on the humerus, but is restricted to its proximal third (Fürbringer, 1876; Ribbing, 1938; Meers, 2003).

The avian M. coracobrachialis consists of two mainly independent heads, M. coracobrachialis cranialis and M. coracobrachialis caudalis. However, Sullivan (1962) showed that the latter muscle is embryologically derived from the M. subcoracoscapularis system and will therefore be discussed below (see ‘M. subcoracoscapularis’ below). In ratites, the fleshy origin of the large M. coracobrachialis cranialis is located on the dorsolateral edge of the coracoid immediately cranioventral to the glenoid (Fürbringer, 1888, 1902; McGowan, 1982; Nicholls and Russell, 1985). As in other tetrapods, it inserts on the proximal ventral surface of the humerus. In carinates, the origin of the relatively small M. coracobrachialis cranialis has shifted cranially, and is restricted to the lateral side of the acrocoracoid process and to the Ligamentum acrocoracohumerale (Fürbringer, 1902). The muscle has a fleshy insertion on the proximal cranial (developmentally ventral) side of the humerus within the Impressio coracobrachialis, a well-defined osteological correlate of this muscle (Fürbringer, 1888, 1902; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; McGowan, 1986; Vanden Berge and Zweers, 1993).

DISCUSSION – Nicholls and Russell (1985) interpreted the crocodilian M. coracobrachialis brevis ventralis as a homologue of the lepidosaurian M. coracobrachialis longus, but the insertion of both parts of M. coracobrachialis at the proximal end of the humerus renders this interpretation improbable. Fürbringer (1888, 1902) and Romer (1944) demonstrated the homology of the avian M. coracobrachialis cranialis to M. coracobrachialis brevis. Therefore, the EPB implies that M. coracobrachialis longus was already lost in basal archosaurs.

Since the origin of M. coracobrachialis brevis is mainly fleshy, and birds strongly modified the coracoid and its muscles, the exact area of origin of this muscle is hard to delimit in extinct forms. However, phylogenetic inference implies that it was situated on the lateral surface of the coracoid, between the origins of M. biceps brachii and M. supracoracoideus. In both crocodilians and birds, the site of origin has shifted cranially relative to the plesiomorphic condition, but Fürbringer (1902) regarded these developments as convergent. On the other hand, Romer (1922) already remarked the constancy of the insertion of M. coracobrachialis brevis (= cranialis) within a depression on the developmentally ventral proximal humerus. This depression is also present in extinct archosaurs. Therefore, interpreting this structure as the site of insertion of M. coracobrachialis brevis is a Level I inference.

11. M. supracoracoideus (SC).

Synonyms:

M. pectoralis secundus (MacAlister, 1864)
M. pectoralis minor, M. supraspinatus (Haughton, 1866)
M. epicoraco-humeralis, M. subclavius (Mivart, 1867, 1870)
M. supraspinatus (Sanders, 1870, 1872, 1874)
M. epicoracohumeralis (de Vis, 1884; Byerly, 1925; Cong et al., 1998)
M. coracohumeralis (Rabl 1916)
M. coracobrachialis brevis dorsalis (for scapular head) (Meers, 2003)

Remarks: The homology of this muscle has been a matter of debate among the anatomists of the 19th century, resulting in a multitude of differing names. The current term 'M. supracoracoideus' was established by Fürbringer (1876, 1888) for non-avian reptiles and birds, and has been adopted by almost all following ornithologists. Therefore, the NAA also uses this term in its standardized terminology (Vanden Berge and Zweers, 1993).

DESCRIPTION – Like M. coracobrachialis brevis, M. supracoracoideus (figs. 3-6, 3-7) is characterized by a relatively constant site of insertion, and a varying area of origin. The amphibian homologue of this muscle arises from a large portion of the lateral side of the coracoid and inserts onto the apex of the deltopectoral crest, proximal to the insertion of M. pectoralis. A second insertion is situated just cranial to the humeral head (Miner, 1925; Francis, 1934; Walthall and Ashley-Ross, 2006). In *Sphenodon*, the muscle is relatively large and strongly coadunate with M. coracobrachialis brevis. Its origin is located on the cranial half of the lateral side of the coracoid. The muscle inserts on the lateral tuberosity on the proximal base of the deltopectoral crest, and on the ventral part of the Ligamentum scapulohumerale laterale (Fürbringer, 1900; Miner, 1925; Ribbing, 1938). Most squamates show a similar morphology, but the cranial coracoid fenestra perforates the squamate coracoid in the area of the M. supracoracoideus attachment. Thus, the muscle arises from the edges of this opening. M. supracoracoideus inserts on the proximal base of the deltopectoral crest next to the lateral tuberosity (Mivart, 1867; Sanders, 1870, 1872; Fürbringer, 1876, 1900; de Vis, 1884; Rabl, 1916; Ribbing, 1938). Chameleons exhibit a modified morphology: M. supracoracoideus is partially displaced dorsally and differentiated into a ventral and a dorsal head, the latter arising from up to two thirds of the lateral side of the scapula (Mivart, 1870; Fürbringer, 1876, 1900).

In crocodilians, M. supracoracoideus is subdivided into a coracoidal and a scapular head. In this respect, it resembles the condition seen in chameleons. The coracoidal part arises from the entire cranial half of the coracoid, including its medial side, and inserts next to pars scapularis on the apex of the deltopectoral crest (Fürbringer, 1876, 1900; Ribbing, 1938; Cong et al., 1998). Meers (2003) subdivided this muscle into three heads (Mm. supracoracoidei brevis, intermedius et longus). However, Nicholls and Russell (1985) found only a single head arising from the medial side of the coracoid, and Jasinoski et al. (2006) were not able to identify a M. supracoracoideus brevis in their specimens. Apparently, the origin of the ventral part of M. supracoracoideus is subject to substantial variation. The scapular part of M. supracoracoideus has its origin on the ventral third of the lateral side of the scapula, and may insert somewhat more proximal to pars coracoideus on the base of the deltopectoral crest (Meers, 2003; Jasinoski et al., 2006).

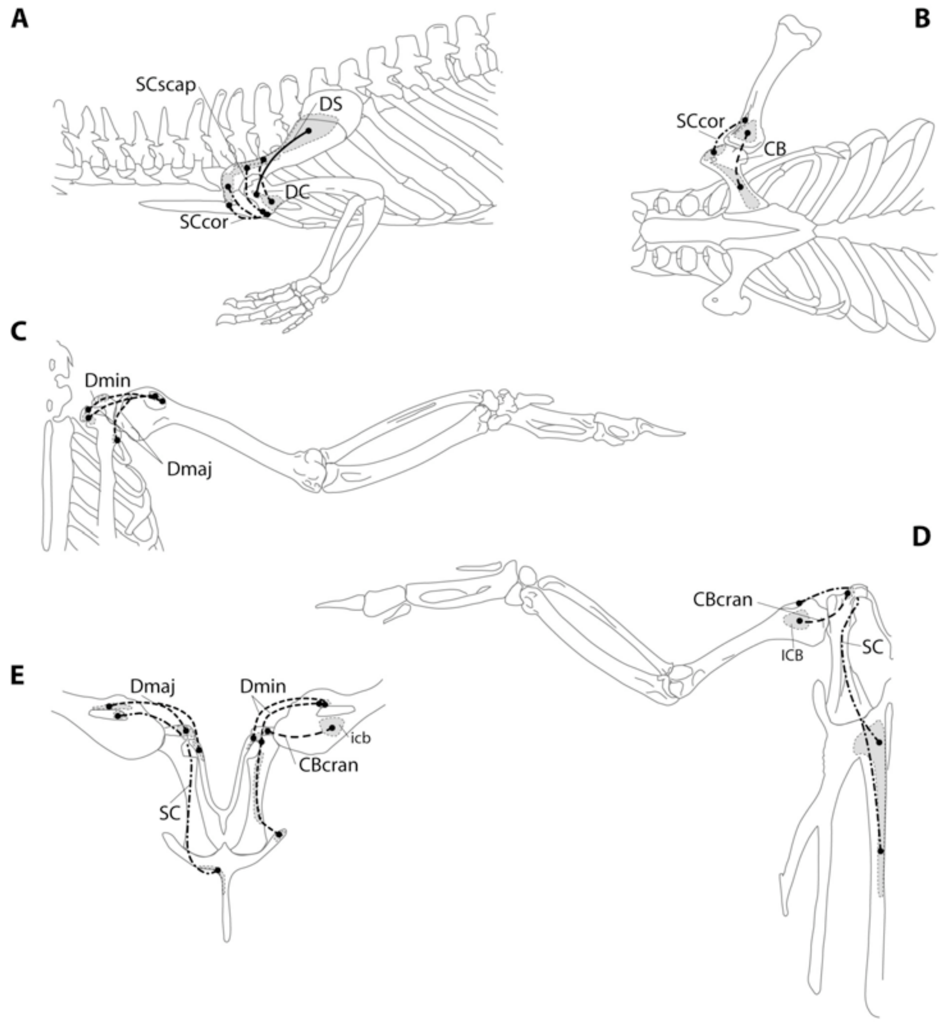

Figure 3-7. Superficial humeral muscles arising from the pectoral girdle in *Alligator* (A, left lateral view; B, ventral view) and *Gallus* (C, dorsal view; D, ventral view; E, cranial view). Shaded lines of action indicate that the course of a muscle is on the remote side of the respective bony element.

The avian M. supracoracoideus is strongly enlarged. It is one of the most important flight muscles and serves as the primary wing elevator. Almost all birds retain a fleshy origin of this muscle from the coracoid, but the main part of M. supracoracoideus has extended caudally to arise from the ventral surface and carina of the sternum, deep to M. pectoralis. The coracoidal part of M. supracoracoideus arises in most cases from the medioventral part of the coracoid, where it is separated from the origin of M. coracobrachialis caudalis by an intermuscular ridge (Baumel and Witmer, 1993). All fibers of M. supracoracoideus converge into a strong tendon that wraps around the acrocoracoid, runs through the triosseal foramen and inserts onto the lateral tuberosity of the humerus (Fürbringer, 1888, 1902; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; Schreiweis, 1982; McGowan, 1986). Fürbringer (1886) noted a positive correlation between the size of M. supracoracoideus and the size of the acrocoracoid process. In ratites other than *Rhea*, the origin of this muscle is restricted to the lateral side of the coracoid, but its point of insertion is the same as in carinates (Fürbringer, 1888, 1902; Gadow and Selenka, 1891; McGowan, 1982; Nicholls and Russell, 1985).

DISCUSSION – A single-headed origin from the craniolateral side of the coracoid seems to constitute the plesiomorphic condition of M. supracoracoideus. Fürbringer (1900) speculated that the fusion of M. supracoracoideus and M. coracobrachialis brevis seen in *Sphenodon* might be plesiomorphic for diapsids. A subdivision into a coracoidal head and a scapular head as in chameleons, turtles (Walker, 1973) and crocodilians is hence derived. Since birds do not have a scapular head of this muscle, phylogenetic inference cannot answer the question if the condition found in crocodilians is close to the plesiomorphic archosaurian morphology, or is unique to this group. Therefore, some speculation is needed to decide if basal archosaurs possessed a scapular division of M. supracoracoideus (level II inference), but the reconstruction of neighboring muscles and the structure of the scapula in these forms support this model (chapter 4). Moreover, under the assumption of a sister group relationship between archosaurs and chelonians (Zardoya and Meyer, 1998; Hedges and Poling, 1999; Kumazawa and Nishida, 1999; Rest et al., 2003; Iwabe et al., 2005; Matsuda et al. 2005), outgroup comparison also strengthens such a reconstruction. Accordingly, the scapular head would be secondarily lost in birds, as a consequence of the reduction and reorientation of the proximal scapula.

12. M. pectoralis (P).

Synonyms:

M. pectoralis major (Haughton, 1866; Mivart, 1867, 1870; Sanders, 1870, 1872, 1874; de Vis, 1884)

M. pectoralis superficialis (Fisher, 1946; Fisher and Goodman, 1955)

Remarks: This muscle is uniformly named M. pectoralis in all tetrapods. However, different epithets exist in the literature, because early anatomists regarded other ventral shoulder muscles as part of M. pectoralis system (e.g., M. supracoracoideus). In birds, there are two additional muscular slips derived from M. pectoralis. Accordingly, the NAA distinguishes between M. pectoralis sternobrachialis (M. pectoralis thoracicus of earlier authors), M. pectoralis costobrachialis (M. pectoralis abdominalis), and M. pectoralis propatagialis (Vanden Berge and Zweers, 1993).

DESCRIPTION – The large M. pectoralis (figs. 3-8, 3-9, 3-10) is situated on the ventral side of the tetrapod body, and is a powerful adductor and retractor of the forelimb. In all tetrapods, it inserts distally on the caudal side of the deltopectoral crest. Its primary origin is the ventral surface of the sternum, but it may also extend caudally onto M. rectus abdominis in amphibians (Miner, 1925; Francis, 1934; Ribbing, 1938; Walthall and Ashley-Ross, 2006). The anuran M. pectoralis has a cranial extension onto the coracoid (Ribbing, 1938).

In *Sphenodon*, the origin of this muscle is more extensive than in amphibians and includes the dermal parts of the shoulder girdle and abdomen. M. pectoralis arises from the lateral surface of the clavicle, from the ventral sides of the interclavicle and sternum, from the medial ends of the sternal ribs, and from the cranial 15-17 gastralia (Fürbringer, 1900; Byerly, 1925; Miner, 1925; Ribbing, 1938). A similar arrangement is found in squamates, but the origin from the clavicle is present only in few forms (e.g., Sanders, 1872; de Vis, 1884; Rabl, 1916). The posterior extension of M. pectoralis is restricted to sternal ribs 2 to 4 in Squamata (Fürbringer, 1900; Ribbing, 1938).

The crocodilian M. pectoralis retains its origin from the interclavicle, almost the entire sternum, and sternal ribs 1 to 8 (Fürbringer, 1876; Meers, 2003). Meers (2003) noted a differentiation into a cranial and a caudal division, the latter sometimes extending onto the gastralia. In *Alligator sinensis,* Cong et al. (1998) identified an additional head of this muscle that connects to the pelvic region, and named it M. pectoralis abdominalis (a superficial slip similar to that found in birds, see below). However, this derivate could not be found in *Caiman* (own observation) and is not reported by other authors.

In carinate birds, M. pectoralis usually is the largest muscle of the body and the primary wing depressor. Additional to the large sternobrachial part, there are also two small slips that run to the pelvic region (pars abdominalis) and control the propatagium (pars propatagialis). M. pectoralis arises from the entire sternum, with the exception of the dorsomedial parts covered by M. supracoracoideus, and extends also onto the lateral side of the furcula (Fürbringer, 1888, 1902; Hudson and Lanzilloti, 1955; Berger, 1966; Schreiweis, 1982; Vanden Berge and Zweers, 1993). In some forms, M. pectoralis is differentiated into a superficial and a deep layer (Fisher, 1946; Fisher and Goodman, 1955). Hudson and Lanzilloti (1964) found the muscle to be extended onto the lateral sides of the first three sternal ribs.

M. pectoralis is reduced in ratites, its origin being restricted to the lateral region of the sternum and the adjacent ventrolateral part of the coracoid (the latter part is missing in *Struthio*). These forms also lack pars propatagialis and, with the exception of *Apteryx*, pars abdominalis.

DISCUSSION – M. pectoralis is easy to homologize and is correlated with an unambiguous osteological feature at its insertion, the distal part of the deltopectoral crest. Therefore, it can be concluded that the muscle arose from the sternum and inserted into the deltopectoral crest in basal archosaurs, too. More speculation is necessary for an assessment of the cranial and caudal extent of its origin. Romer (1922) and Miner (1925) concluded that interclavicular and clavicular origins are plesiomorphic for tetrapods, but were lost in modern amphibians. Since a clavicular origin is present both in birds and in *Sphenodon*, whereas crocodilians lost their clavicles but retained an origin of M. pectoralis from the interclavicle, it is possible that in basal archosaurs this muscle also connected to the clavicles. The caudal extent of M. pectoralis is hard to reconstruct, because its fleshy origin does not leave clear osteological correlates on the sternal ribs and gastralia; moreover, these elements are seldomly preserved in fossil forms. Nevertheless, Fürbringer (1900) assumed that the well-developed gastral apparatus found in many fossil amniotes might have served as an anchor for M. pectoralis. Crocodilians would then have lost this site of origin, in conjunction with a reduction of the gastralia.

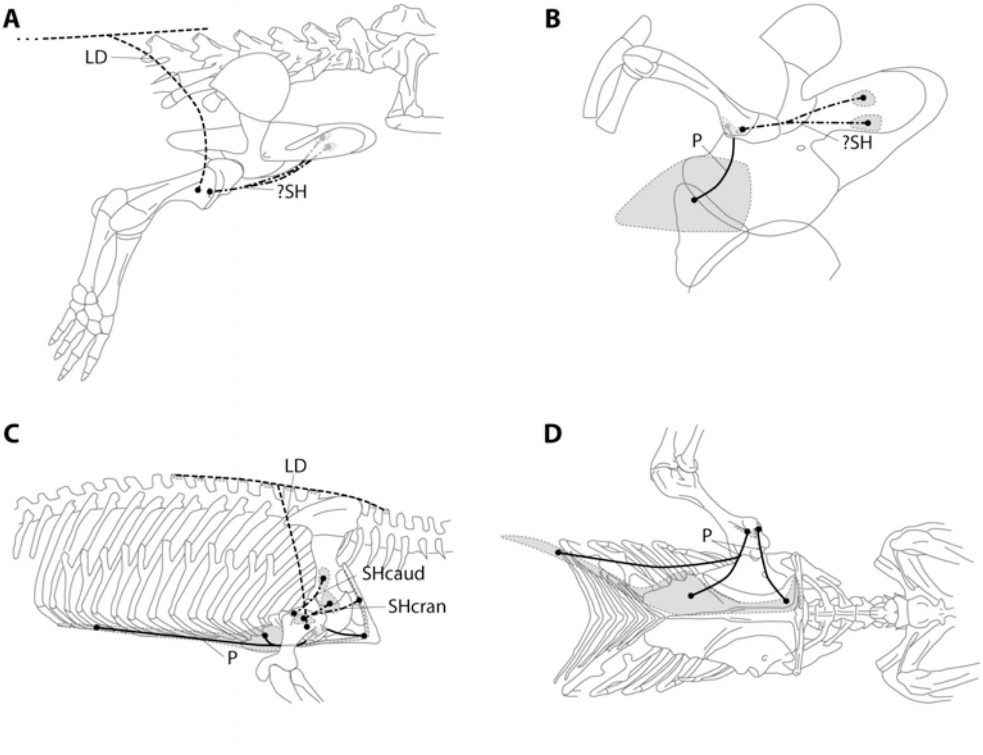

Figure 3-8. M. latissimus dorsi, M. pectoralis and the Mm. scapulohumerales complex of urodeles (A, right lateral view; B, ventral view) and *Sphenodon* (C, right lateral view; D, ventral view). There is no M. teres major in these groups.

13. M. latissimus dorsi (LD).

Synonyms:

M. dorso-humeralis (Fürbringer, 1876; Francis, 1934)

Remarks: Fürbringer (1876) is the only author who suggested a deviant name for this muscle, based on his topological nomenclature. However, his system never became widely accepted in the literature.

DESCRIPTION – M. latissimus dorsi (figs. 3-8, 3-9, 3-10) is the only muscle that spans between the dorsal axial skeleton and the humerus. It is present in all tetrapods (Romer, 1922). In amphibians, the muscle arises from the dorsal fascia and partially from the transverse processes and neural spines in the cranial trunk region (Miner, 1925; Francis, 1934; Ribbing, 1938; Walthall and Ashley-Ross, 2006). It merges with other soft tissue structures and does not reach the surface of the humerus in some forms (Miner, 1925), but in others, in inserts by a strong tendon on the dorsal humerus just caudal to the deltopectoral crest (Francis, 1934; Walthall and Ashley-Ross, 2006).

A strong tendinous insertion of this muscle on the dorsal side of the humerus is also present in almost all non-avian Reptilia. The tendon of insertion is shared with M. teres major, if the latter muscle is present. M. latissimus dorsi of *Sphenodon* has a wide aponeurotic origin that may extend over the neural spines of the last three cervical and nine dorsal vertebrae. The muscle narrows down to a strong tendon that passes between the scapular and medial humeral heads of M. triceps brachii (see below, 'M. triceps brachii'), and variably inserts onto the proximal half of the dorsal side of the humerus (Fürbringer, 1900; Miner, 1925). Quite a similar morphology is seen in squamates, which indeed often lack a M. teres major (Mivart, 1867; Sanders, 1870, 1872; Fürbringer, 1876, 1900; Rabl, 1916). The craniocaudal extent of M. latissimus dorsi is reduced in chameleons (Mivart, 1870; Fürbringer, 1876, 1900; Ribbing, 1938) and some other forms (Sanders, 1874; de Vis, 1884) to three or four dorsal vertebrae.

The crocodilian M. latissimus dorsi has a short aponeurotic origin from the level of dorsal vertebrae 1 to 5, leading to a muscle that is comparatively weaker than in most lepidosaurs. Like in lepidosaurs, the tendon of insertion passes between two heads of M. triceps brachii, fuses with the tendon of M. teres major, and inserts onto the proximal dorsal side of the humerus, where it usually leaves a prominent scar, tubercle or depression (Meers, 2003). M. latissimus dorsi exhibits a slight differentiation into a cranial and a caudal part at its origin (Fürbringer, 1876; Cong et al., 1998).

The avian M. latissimus dorsi is much more specialized than the corresponding muscle of other tetrapods. It consists of three independent heads, pars metapatagialis (a dermal aberration that controls the metapatagium), pars cranialis, and pars caudalis. The latter two heads may fuse in some forms (Fürbringer, 1900; McGowan, 1986). In most birds, pars cranialis arises aponeurotically from the neural spines of the last cervical and two or three cranial dorsal vertebrae (Fürbringer, 1888, 1902; Hudson and Lanzilloti, 1955; Schreiweis, 1982; McGowan, 1986). In galliforms, the origin is level with the last two cervicals and the first dorsal (Hudson and Lanzilloti, 1964). Its elongate, tendinous insertion on the caudal (developmentally dorsal) side of the humerus is correlated with a distinct ridge (Fürbringer, 1902). The caudal part of M. latissimus dorsi usually is stronger than the cranial part and takes origin from the neural spines of the caudal dorsal vertebrae, as well as from the cranial edge of the ilium. Like pars cranialis, it passes between M. scapulotriceps and M. humerotriceps on its way to the dorsal side of the humerus. Its insertion is often separate from that of pars cranialis and sometimes associated with a bony eminence. In other forms, pars caudalis does not reach the humerus but connects to the M. triceps brachii complex (Galliformes, Hudson and Lanzilloti, 1964), or it fuses with M. latissimus dorsi pars cranialis (Cathartidae, Fisher, 1946).

In contrast to the condition found in neognaths, the ratite M. latissimus dorsi pars caudalis usually is smaller than pars cranialis (Fürbringer, 1888, 1902). In *Rhea* and *Dromaius*, it lost its connection to the dorsal fascia and arises from one or two thoracic ribs (Gadow and Selenka, 1891). Only in *Struthio,* an aponeurotic origin from dorsal vertebrae 6 to 8 and the ilium is retained (Gadow and Selenka, 1891). *Apteryx* shows no differentiation into a cranial and a caudal part (Fürbringer, 1888, 1902); however, McGowan (1982) stated that pars cranialis is completely lost in this form. In the remaining ratites, the origin of M. latissimus dorsi pars cranialis does not extend to the cervical vertebrae. In *Rhea, Dromaius*, and *Casuarius*, there is also a small muscle arising from the scapula that fuses to pars cranialis, and potentially is a homologue of M. teres major (Fürbringer, 1902; Ribbing, 1938; see Discussion below, and section 'M. teres major').

DISCUSSION – M. latissimus dorsi is a constant feature of all tetrapods (Romer, 1922). Since its tendinous insertion is associated with an osteological correlate in both extant bracket taxa and also in other amniotes, it is a level I inference to identify a similar structure on the dorsal side of the humerus of extinct archosaurs as the point of attachment of this muscle. It can also be concluded that in these forms the tendon of insertion passed between the scapular and the medial head of

M. triceps brachii. A differentiation of M. latissimus dorsi into a cranial and a caudal part is possible for basal archosaurs (level II inference), but not probable (chapter 4). It should also be noted here that Fürbringer (1886, 1902) suggested that the avian M. latissimus dorsi cranialis might indeed represent a homologue of M. teres major, rendering the caudal part of M. latissimus dorsi the only true homologue of the reptilian muscle (see below, 'M. teres major'). Given its origin from the dorsal fascia and the lack of clear osteological correlates, the craniocaudal extent of M. latissimus dorsi cannot be reconstructed reliably in extinct archosaurs.

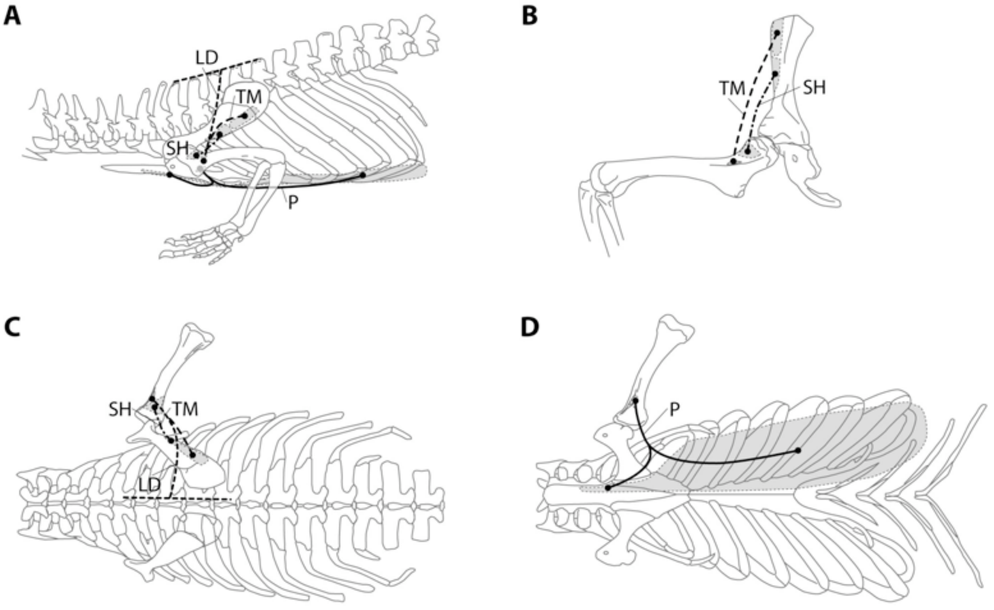

Figure 3-9. M. pectoralis, M. latissimus dorsi, M. teres major, and M. scapulohumeralis (caudalis) of *Alligator*. Shaded attachment areas and lines of action indicate muscles that lie on the remote side of the respective bone.

14. M. teres major (TM).

Synonyms:

M. teres (Ribbing, 1938)

Remarks: Although a direct homology of this muscle to the mammalian M. teres major is doubtful (see below, Discussion), all modern authors apply this term also for diapsids. The present thesis follows this convention.

DESCRIPTION – M. teres major (fig. 3-9) is a specialized part of M. latissimus dorsi (Fürbringer, 1876, 1900; Romer, 1922) that takes origin from the caudodorsal part of the lateral side of the scapular blade. It is missing in amphibians, *Sphenodon*, and most squamates, with the exception of some agamids (e.g., *Uromastyx*), where it arises from the caudal part of the suprascapula, or the caudal edge of the scapula (Fürbringer, 1876, 1900). The insertion of this muscle is located proximally on the dorsal side of the humerus, next to the medial tuberosity. The tendon of insertion is shared with that of M. latissimus dorsi (Fürbringer, 1900). M. teres major is also present in many chelonians (especially pleurodirans), where it arises from almost the whole length of the lateral side of the scapula prong. As in crocodilians, its tendon of insertion fuses to that of M. latissimus dorsi (Ribbing, 1938; Walker, 1973).

In crocodilians, M. teres major is comparatively well developed and equals M. deltoideus scapularis in size. It arises fleshy from the caudodorsal region of the lateral side of the scapula, in some forms also having contact to the suprascapular cartilage. As mentioned above, it inserts together with M. latissimus dorsi by a strong tendon on the proximodorsal side of the humerus, leaving a distinct scar (Haughton, 1866; Fürbringer, 1876; Ribbing, 1938; Cong et al., 1998; Meers, 2003).

Most birds have lost M. teres major. Only in *Rhea,* a small muscle arises from the dorsal part of the scapula blade, and fuses with M. latissimus dorsi cranialis prior to their common insertion (Fürbringer, 1886, 1888, 1902; see also above, 'M. latissimus dorsi').

DISCUSSION – As noted by Fürbringer (1876, 1900) and Romer (1922), a M. teres major is a specialized part of M. latissimus dorsi that shifted its origin onto the dorsal part of the scapula. Since the cranial part of M. latissimus dorsi is always close to the scapula, it is easy to imagine how a M. teres major might have evolved independently several times in tetrapod history. The distribution of this muscle among extant tetrapods suggests that it formed at least four times, in mammals, agamids, archosaurs, and chelonians. It is also possible that the muscle seen in *Rhea* and the crocodilian counterpart are independent developments. However, according to the amniote phylogeny suggested by recent molecular studies (Zardoya and Meyer, 1998; Hedges and Poling, 1999; Kumazawa and Nishida, 1999; Rest et al., 2003; Iwabe et al., 2005; Matsuda et al. 2005), the presence of M. teres major may also be a synapomorphic character of Chelonia + Archosauria that was secondarily lost in most birds. Fürbringer (1886, 1902) made the suggestion that the avian M. latissimus dorsi cranialis may indeed represent a modified M. teres major that extended its origin dorsally onto the dorsal fascia. However, embryological examinations (Sullivan, 1962) could not find supportive data for this hypothesis. In summary, it is assumed here that M. teres major was present in basal archosaurs, arose fleshy from the caudodorsal part of the scapula, and inserted in common with M. latissimus dorsi. Since it has no unambiguous osteological correlates at its origin, the exact localization of this muscle is somewhat speculative.

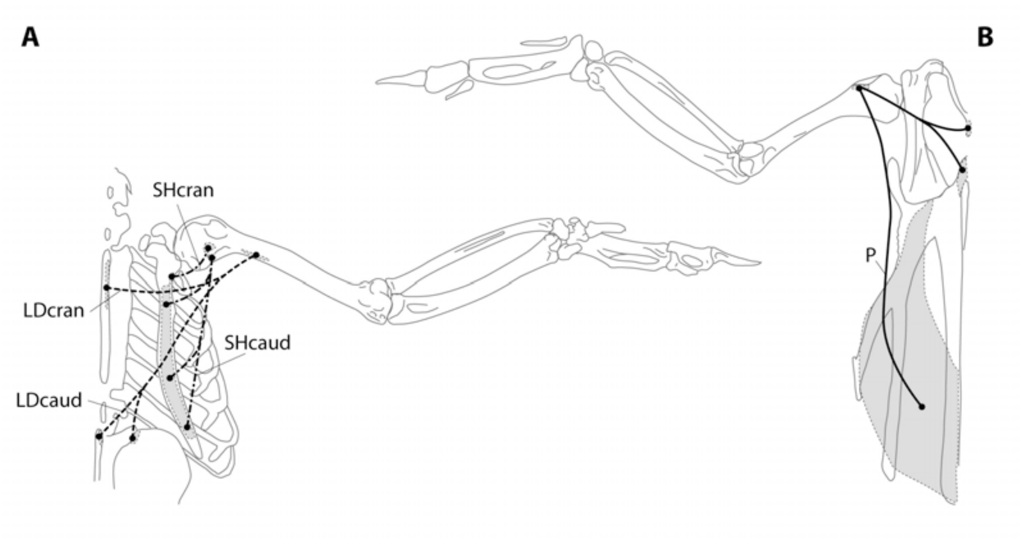

Figure 3-10. M. pectoralis, M. latissimus dorsi and Mm. scapulohumerales in *Gallus*.

15. Mm. scapulohumerales (SH).

Synonyms:

M. infraspinatus (Mivart, 1867; de Vis, 1884)
M. suprascapularis posterior (Mivart, 1870)
M. teres minor (Sanders, 1870, 1872)
M. scapulo-humeralis profundus (Fürbringer, 1876)
M. proscapulohumeralis brevis, M. dorsalis scapulae (Fisher, 1946; Fisher and Goodman, 1955; Berger, 1953, 1954, 1955, 1956a–c, 1957, 1960, 1966)

Remarks: The long list of synonyms for the scapulohumeral muscles results from a dispute on the homology of this complex. However, modern workers on crocodilian anatomy (Cong et al., 1998; Meers, 2003) as well as the NAA (Vanden Berge and Zweers, 1993) adapt Fürbringer's (1900, 1902) nomenclature and use the term M. scapulohumeralis, without questioning the derivation of the two avian muscles (M. scapulohumeralis cranialis and M. scapulohumeralis caudalis) from a common origin.

DESCRIPTION – The Mm. scapulohumerales complex (figs. 3-8, 3-9, 3-10) consists of two muscles, M. scapulohumeralis cranialis and M. scapulohumeralis caudalis. At least one of these two muscles is present in all sauropsids, with the exception of turtles (Walker, 1973). A similar, single muscle is present in caudate amphibians (Miner, 1925), but mammals other than *Echidna* show no traces of M. scapulohumeralis (Ribbing, 1938).

The key taxon for the reconstruction of the plesiomorphic condition of Mm. scapulohumerales is *Sphenodon* (Fürbringer, 1900). In this animal, the muscle retains both a cranial and a caudal head. M. scapulohumeralis cranialis arises from the dorsal part of the coracoid and the ventral part of the scapula. It also has a second origin by a deeper, small muscular slip that comes from the caudal edge of the scapula. The fleshy insertion on the dorsoproximal humerus is situated between that of M. latissimus dorsi and the medial tuberosity. M. scapulohumeralis caudalis is smaller than the cranial head, and arises dorsally to the latter on the ventral half of the scapula. Both muscles are separated from each other by M. triceps brachii caput scapulare. Pars caudalis inserts medially to the cranial part on the distal end of the medial tuberosity (Fürbringer, 1900; Byerly, 1925; Miner, 1925).

Other extant lepidosaurs have completely lost M. scapulohumeralis caudalis (Fürbringer, 1900). The remaining M. scapulohumeralis (cranialis) is relatively small, but retains its origin from the caudal part of the ventral scapula and dorsal coracoid, i.e. from the rim of the coracoscapular fenestra. Only in *Chamaeleon,* its origin is restricted to the caudal edge of the ventral scapula. Like in *Sphenodon*, the squamate M. scapulohumeralis has a fleshy insertion proximomedially on the dorsal humerus (Mivart, 1867; Sanders, 1870, 1872; Fürbringer, 1876, 1900; de Vis, 1884; Rabl, 1916).

In contrast to squamates, crocodilians lost M. scapulohumeralis cranialis and retained M. scapulohumeralis caudalis. Its origin is restricted to the caudal edge and caudolateral margin of the ventral third of the scapula. Running over the articular capsule, it inserts right distally to the medial tuberosity, next to M. subscapularis and between two of the humeral heads of M. triceps brachii (Fürbringer, 1876, 1900; Ribbing, 1938; Cong et al., 1998; Meers, 2003).

Most carinate birds preserved both parts of M. scapulohumeralis, but pars cranialis is frequently lost, e.g. in *Columba* (Berger, 1966). The muscle arises from the ventral part of the collum scapulae, just distal to the glenoid, but may extent caudally up to one fifth of the length of the scapular blade. It inserts onto the proximal dorsal humerus, just distolateral to the pneumatic fossa, where it may be correlated with a bony eminence. M. scapulohumeralis caudalis usually is wider than pars cranialis, having a fleshy origin from most of the lateral surface of the scapular blade except its cranial quarter and caudal tip. The muscle has a tendinous insertion distomedially on the medial tuberosity (Fürbringer, 1888, 1902; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; McGowan, 1986; Vollmerhaus et al., 1992; Vanden Berge and Zweers, 1993).

Ratites have substantially reduced or completely lost M. scapulohumeralis cranialis (Gadow and Selenka, 1891; Fürbringer, 1902; McGowan, 1982; Berger, 1966). Pars caudalis has a less extended origin that is restricted to the ventral edge of the scapular blade, but *Struthio* and *Rhea* have a wider insertion distal to the medial tuberosity than most carinates (Fürbringer, 1888, 1902).

DISCUSSION – Although some authors assumed that Mm. scapulohumerales are independent specializations of M. supracoracoideus (pars cranialis, Romer, 1922), Mm. deltoidei (Miner, 1925; Ribbing, 1938), or M. subscapularis (pars caudalis, Fürbringer, 1900), embryological examinations revealed that both muscles differentiate from a single primordial muscle mass (Sullivan, 1962). Under consideration of the situation met in *Sphenodon* and birds, it must be concluded that basal archosaurs had both a cranial and a caudal part of M. scapulohumeralis. Due to its mainly fleshy nature, pars cranialis has no unambiguous osteological correlates in *Sphenodon* and most birds. However, Jasinoski et al. (2006) reported an oval scar that correlates to the origin of this muscle in *Cygnus* and identified a similar structure in dromaeosaurids. The origin of M. scapulohumeralis caudalis is varying in *Sphenodon*, crocodilians, and birds; therefore, its localization in extinct archosaurs requires some speculation. Since the areas of insertion of both Mm. scapulohumerales are relatively constant in all diapsids, it is a Level I inference to identify the distal part of the medial tuberosity as the site of insertion of the caudal head, and to reconstruct the cranial head to have inserted between this tuberosity and the scar of M. latissimus dorsi.

16. M. subcoracoscapularis (SCS).

Synonyms:

M. scapulo-humeralis posterior (Romer, 1922)
M. subscapularis, M. teres major (Rabl, 1916)
M. subscapulo-coraco-brachialis (Byerly, 1925)
M. subscapularis, M. subcoracoideus, M. coracobrachialis caudalis (see remarks)

Remarks: This muscle complex, which plesiomorphically arises by two heads from the coracoid and the scapula, has been substantially modified in archosaurs. It is differentiated into three or more independent parts in birds (M. subscapularis, M. subcoracoideus, M. coracobrachialis caudalis), while crocodilians retained a scapular head only (M. subscapularis). Hence, NAA and crocodilian nomenclature cannot properly reflect the plesiomorphic condition that was present in basal archosaurs. Therefore, in accordance with Dilkes (2000), Fürbringer's (1900) subsuming name for this muscle complex is preferred throughout this thesis.

DESCRIPTION – The caudatan M. subcoracoscapularis (fig. 3-11) arises from the ventral third of the medial side of the scapula and the adjacent coracoid. A comparable muscle is missing in anurans (Miner, 1925; Francis, 1934; Ribbing, 1938).

Most diapsids, with the exception of crocodilians, exhibit a differentiation of M. subcoracoscapularis into two portions, a caudal head ('M. subcoracoideus'), and a scapular head ('M. subscapularis'). The Ligamentum sternoscapulare internum runs between both heads. However, this split is not much pronounced in *Sphenodon* (Fürbringer, 1900; fig. 3-11). In this form, pars coracoideus has a fleshy origin from the majority of the inner side of the coracoid, while the small pars scapularis comes from the caudoventral edge and adjacent medial side of the scapula. Both heads soon fuse and insert with a common tendon onto the medial tuberosity of the humerus (Fürbringer, 1900; Miner, 1925). In other lepidosaurs, the area of origin of M. subcoracoscapularis is much enlarged and covers almost the complete inner surface of the shoulder girdle, including the ventral part of the suprascapular cartilage. In some forms, pars scapularis wraps around the caudal border of the scapula, and arises in part also from its lateral face (Mivart, 1867; Sanders, 1870, 1872, 1874; Fürbringer, 1876, 1900; de Vis, 1884; Rabl, 1916; Ribbing, 1938). In other forms, like chameleons, both heads are smaller and clearly separate at their origins, but always fuse towards their common insertion on the medial tuberosity (Mivart, 1870; Fürbringer, 1876, 1900).

Turtles have lost the coracoidal head of this muscle complex, but the remaining head (M. subscapularis) is well developed and clasps around the medial, caudal, and lateral parts of the scapular prong (fig. 3-12). As in other tetrapods, the muscle inserts via a tendon on the medial tuberosity of the humerus (Ribbing, 1938; Walker, 1973). Crocodilians also have lost pars coracoideus, while the large scapular head (M. subscapularis) arises from almost the entire medial surface of the bony scapula (fig. 3-12). Its insertion on the medial tuberosity is somewhat extended distally onto the base of that process (Haughton, 1866; Fürbringer, 1876, 1900; Cong et al., 1998; Meers, 2003).

In contrast to crocodilians and turtles, birds retain a coracoidal head of M. subcoracoscapularis, and exhibit a novel derivate known as M. coracobrachialis caudalis (Sullivan, 1962; see Discussion below). Furthermore, pars scapularis (M. subscapularis) is subdivided into a medial and a lateral head in most birds (fig. 3-12). The fleshy origin of the coracoidal head (M. subcoracoideus) may cover the complete medial side of the coracoid, but in many birds it is restricted to the proximal, the middle, or the distal third of that bone (Fürbringer, 1902; Fisher, 1946). Ratites are no exception in this respect (MacAlister, 1866; Fürbringer, 1888, 1902; Gadow and Selenka, 1891; McGowan, 1982). In galliforms and penguins, the muscle also has a fleshy origin from the craniodorsal side of the sternum (Hudson and Lanzilloti, 1964; Schreiweis, 1982). In some forms, M. subcoracoideus has differentiated into two individual heads (Hudson and Lanzilloti, 1955; Berger, 1966; Vollmerhaus et al., 1992).

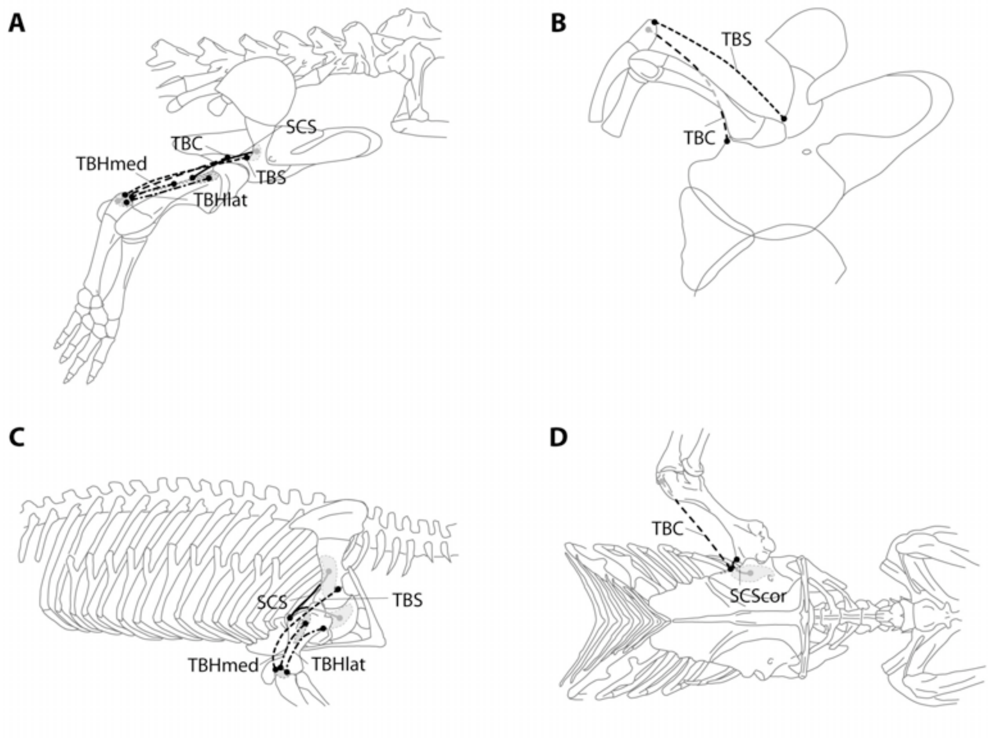

Figure 3-11. M. subcoracoscapularis and M. triceps brachii complex of caudatan amphibians (A, lateral view; B, ventral view) and *Sphenodon* (C, lateral view; D, ventral view). Shaded attachment areas and lines of action indicate muscles that lie on the remote side of the respective bone.

The medial head of M. subscapularis arises fleshy from about the proximal half of the medial side of the scapula, including the acromion process. The lateral head is restricted to the proximal half of the scapular blade, where it arises from its ventral border and in some forms also from its lateral face (Fürbringer, 1902; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; Schreiweis, 1982; McGowan, 1986; Vollmerhaus et al., 1992). In ratites, both heads immediately fuse right after their origin (Gadow and Selenka, 1891). They are weakly developed in *Casuarius* and *Dromaius*, and caput mediale is lost in *Apteryx* (McGowan, 1982). In contrast, these muscles have an extensive origin from the medial side of the shoulder girdle in *Rhea* and *Struthio* (Gadow and Selenka, 1891).

In all birds, the individual heads of the M. subcoracoscapularis complex unite and insert via a common tendon on the medial tuberosity of the humerus (MacAlister, 1866; Fürbringer, 1888, 1902; Gadow and Selenka, 1891; Fisher, 1946; Fisher and Goodman, 1946; Hudson and Lanzilloti, 1955, 1964; Berger, 1953, 1954, 1955, 1956a–c, 1957, 1960, 1966; Schreiweis, 1982; McGowan, 1982, 1986; Vollmerhaus et al., 1992; Vanden Berge and Zweers, 1993).

Neither McGowan (1982) nor Nicholls and Russell (1985) could identify a M. coracobrachialis caudalis in *Apteryx* or *Struthio*, but Gadow and Selenka (1891) and Fürbringer (1888, 1902) noted the presence of this muscle in *Struthio,* and a significant development of this muscle in *Rhea.* The carinate M. coracobrachialis caudalis is well developed and arises from the ventral and lateral sides of the coracoid, the adjacent sternum, and the Ligamentum sternocoracoideum. The muscle is associated with an intermuscular ridge that separates its area of origin from that of M. supracoracoideus (Gadow and Selenka, 1891; Fürbringer, 1902). M. coracobrachialis caudalis inserts by a short and strong tendon on the apex of the medial tuberosity of the humerus in virtually all birds (Fürbringer, 1888, 1902; Ribbing, 1938; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; Schreiweis, 1982; McGowan, 1986; Vollmerhaus et al., 1992).

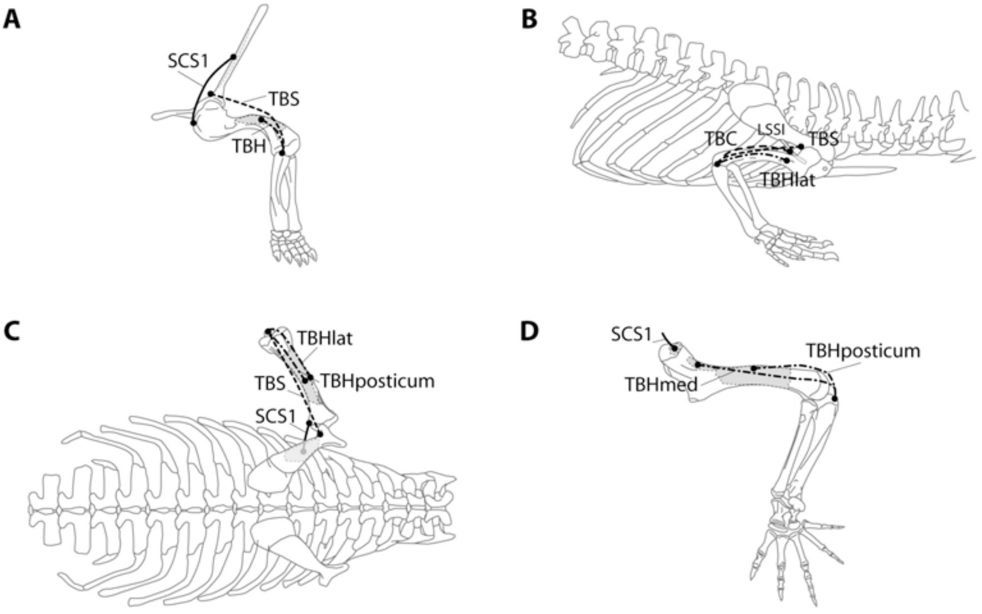

Figure 3-12. M. subscapularis and the M. triceps brachii complex of chelonians (A, lateral view) and *Alligator* (B, lateral view; C, dorsal view; D, caudal view). Shaded attachment areas and lines of action indicate muscles that lie on the remote side of the respective bone.

DISCUSSION – Due to the primarily fleshy origin of all heads of M. subcoracoscapularis, there are no osteological correlates that allow for an unequivocal delimitation of their extent in extinct archosaurs. However, outgroup comparison implies that the last common ancestor of birds and crocodilians had both a coracoidal and a scapular head of M. subcoracoscapularis, covering most of the inner surface of the shoulder girdle and inserting together on the medial tuberosity of the humerus. A different situation is encountered with M. coracobrachialis caudalis. Based on a misinterpretation of the crocodilian M. coracobrachialis brevis ventralis by Nicholls and Russell (1985), Jasinoski et al. (2006) homologized the avian M. coracobrachialis caudalis with M. coracobrachialis longus of non-archosaurian diapsids (compare section 'M. coracobrachialis' above). However, Fürbringer (1902) already noted that the avian M. coracobrachialis caudalis cannot be homologized with any of the related muscles of non-avian sauropsids; instead, it represents a new muscle unique to birds. Sullivan (1962) demonstrated that the muscle is embryologically derived from the M. subcoracoscapularis system (as already indicated by the insertion on the medial tuberosity), but suggested to retain the established name. The correlation of the avian muscle to a distinct intermuscular ridge and to a specialized form of the coracoid indicates that it probably was not present in basal archosaurs, but emerged later in theropod evolution. However, to deny its presence in sauropodomorphs or other dinosaurs is just a Level II inference.

III. Antebrachial muscles.

17. M. triceps brachii (TB).

Synonyms:

- M. extensor cubiti (MacAlister, 1864)
- M. triceps (Haughton, 1866; Mivart, 1867, 1870; Sanders, 1870, 1872, 1874; de Vis, 1884; Romer, 1922; Fisher, 1946; Fisher and Goodman, 1955; Dilkes, 2000; Meers, 2003)
- M. anconaeus (Fürbringer, 1876, 1886, 1888, 1900, 1902; Byerly, 1925; Miner, 1925; Francis, 1934; Walthall and Ashley-Ross, 2006)
- M. extensor ulnae (Ribbing, 1938)
- M. scapulotriceps, M. coracotriceps, M. humerotriceps (Vanden Berge and Zweers, 1993)

Remarks: In order to maintain anatomical preciseness, the annex 'brachii' for 'M. triceps' is retained throughout this thesis, although some recent authors refrained from using it (see synonymy list above). Cong et al. (1998) as well as the first edition of the NAA (Vanden Berge, 1979) also preferred this term. The modern standardized ornithological nomenclature (Vanden Berge and Zweers, 1993) suggests to use the terms 'M. scapulotriceps', 'M. coracotriceps', and 'M. humerotriceps', but since more heads of M. triceps brachii are present in lepidosaurs and crocodilians, this concept cannot be applied to all diapsids. Fürbringer (1876) preferred the term 'M. anconaeus' over 'M. triceps brachii', because the diapsid muscle is no 'triceps' in literal sense, but his concept never became widely accepted in the literature.

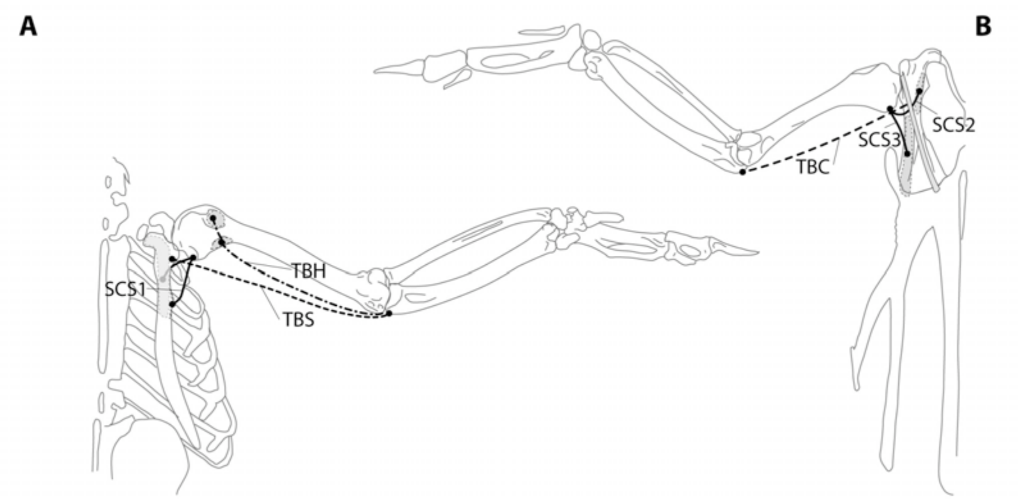

Figure 3-13. The M. subcoracoscapularis and M. triceps brachii complexes of *Gallus* (A, dorsal view; B, ventral view). Shaded attachment areas and lines of action indicate muscles that lie on the remote side of the respective bone.

DESCRIPTION – In most tetrapods, M. triceps brachii (figs. 3-11, 3-12, 3-13) is a complex set of individual muscle heads that fuse distally to end in a common tendon, which inserts on the olecranon process of the ulna. In its plesiomorphic condition, as observed in caudatans and lepidosaurs, M. triceps brachii consists of four parts, a scapular head (M. triceps brachii caput scapulare), a head arising from the coracoid (M. triceps brachii caput coracoideum), and two humeral heads (M. triceps brachii caput humerale mediale, M. triceps brachii caput humerale laterale).

M. triceps brachii caput scapulare (TBS): In amphibians like *Cryptobranchus*, the scapular head arises by a tendon from the caudal edge of the scapula, immediately behind the glenoid. Other forms (e.g., *Necturus*) have an attachment to the shoulder joint capsule only (Miner, 1925; Francis, 1934). In *Sphenodon*, the tendinous origin is placed more cranially, between the cranial and the caudal head of M. scapulohumeralis on the ventral part of the lateral side of the scapula (Fürbringer, 1900; Byerly, 1925; Miner, 1925). In squamates, the muscle has a strong tendon of origin arising from the caudal rim of the scapula immediately behind the glenoid (Sanders, 1870, 1872, 1874; Fürbringer, 1876, 1900; Rabl, 1916; Ribbing, 1938). The muscle may be subdivided into two portions in some forms (Mivart, 1870; Fürbringer, 1876, 1900; de Vis, 1884), and has an additional tendinous origin from the Ligamentum scapulohumerale laterale in others (e.g., *Iguana*: Mivart, 1867; Rabl, 1916).

Turtles and crocodilians have a strong tendinous origin of this muscle, which is located on the scapula directly dorsal to the glenoid (Haughton, 1866; Fürbringer, 1876, 1900; Ribbing, 1938; Walker, 1973; Nicholls and Russell, 1985; Cong et al., 1998), and associated with a prominent scar on the bone (Meers, 2003; Jasinoski et al., 2006; own observation). However, Fürbringer (1876) noted that the course of this muscle relative to other muscles and nerves has shifted laterally, and concluded that it is only in part homologous to the scapular head of M. triceps brachii of lepidosaurs. Like in crocodilians, the avian M. scapulotricpes arises next to the glenoid from the caudal edge of the collum scapulae (Fürbringer, 1902; Hudson and Lanzilloti, 1955; Berger, 1966; Fisher and Goodman, 1964; Schreiweis, 1982; McGowan, 1986), where it is often associated with a tubercle (Baumel and Witmer, 1993). This condition is also found in ratites (MacAlister, 1864; Fürbringer, 1888, 1902; McGowan, 1982). However, in more derived birds the origin of this muscle may extend cranially onto the lateral side of the scapula and even onto the furcula (e.g., in *Gallus:* Fürbringer, 1902; Hudson and Lanzilloti, 1964; Vollmerhaus et al., 1992).

M. triceps brachii caput coracoideum (TBC). The coracoidal head of M. triceps brachii arises by a tendon from the caudal end of the coracoid in amphibians, just medial to M. coracobrachialis longus (Miner, 1925; Francis, 1934). *Sphenodon* exhibits a similar morphology (Fürbringer, 1900; Miner, 1925). In most squamates, the tendon of origin attaches to the entire caudomedial border of the coracoid, in some forms also to the Ligamentum sternoscapulare internum (Mivart, 1867, 1870; Sanders, 1870, 1872, 1874; Fürbringer, 1876, 1900; Ribbing, 1938). However, the coracoidal head is lost in chameleons (Mivart, 1870; Fürbringer, 1876, 1900) and also in chelonians (Ribbing, 1938; Walker, 1973).

In crocodilians, one of the muscular heads of M. triceps brachii is found in a roughly similar position, but it is not regarded as fully homologous to the caput coracoideum of other diapsids (see Discussion below). This head arises from the two branches of the Ligamentum sternoscapulare internum that connect to the caudal margin of the scapula and the caudomedial border of the coracoid, respectively (Haughton, 1866; Fürbringer, 1876, 1900; Ribbing, 1938; Cong et al., 1998; Meers, 2003; Jasinoski et al., 2006). Therefore, the muscle is referred to as M. triceps brachii caput coracoscapulare. On the caudomedial edge of the scapula, the insertion of the internal sternoscapular ligament leaves a rugose scar (Jasinoski et al., 2006; own observation).

In contrast to crocodilians, birds lack a connection of such a muscle to the scapular blade. However, the minute M. coracotriceps arises from a ligament that connects the cranial edge of the sternum and the craniomedial part of the scapulocoracoidal contact. M. coracotriceps remains tendinous over most of its length (Fürbringer, 1902; Berger, 1966; Vanden Berge and Zweers, 1993), and is completely lost in ratites (Fürbringer, 1888, 1902; McGowan, 1982).

M. triceps brachii capiti humerales (TBH). All humeral heads of M. triceps brachii arise fleshy from the dorsal and caudal sides of the humerus. In amphibians, their areas of origin are fluctuating in their extent on the humerus, from a restriction to the proximal quarter (caput humerale laterale of *Cryptobranchus*: Miner, 1925), to an extension over the complete proximodistal length of the shaft (caput humerale mediale of some salamanders: Francis, 1934; Walthall and Ashley-Ross, 2006). In *Sphenodon*, both caput humerale laterale and caput humerale mediale occupy the whole length of the humerus between the insertions of Mm. scapulohumerales and the medial tuberosity proximally, and the articular condyles distally. While the lateral head is situated on the dorsal side of the shaft, the medial head runs down the caudoventral side of the humerus. Proximally, both heads are separated by the areas of insertion of M. latissimus dorsi and Mm. scapulohumerales (Fürbringer, 1900; Byerly, 1925; Miner, 1925). The same morphology is found in squamates. In all lepidosaurs, caput humerale laterale is usually larger than caput humerale mediale (Mivart, 1867, 1870; Sanders, 1870, 1872, 1874; Fürbringer, 1876, 1900; de Vis, 1884; Rabl, 1916; Ribbing, 1938). Chelonians have reduced the medial head of M. triceps brachii, and the remaining M. triceps brachii caput humerale covers the majority of the dorsal side of the humeral shaft (Ribbing, 1938; Walker, 1973). In contrast, crocodilians are specialized by having a third humeral head that is referred to as M. triceps brachii caput humerale posticum. This large, additional head has its origin on the dorsal side of the shaft, between caput humerale laterale and caput humerale mediale. Proximally, the insertion of M. scapulohumeralis caudalis separates this head from the origin of the medial head (Fürbringer, 1876, 1900; Ribbing, 1938; Meers, 2003). In contrast to crocodilians, birds have simplified the humeral part of the M. triceps brachii system. Only one head is retained (M. humerotriceps), but this muscle may be subdivided into a cranial and a caudal part proximally at the level of the pneumatic fossa. The muscle has its origin on the caudodorsal side of the humeral shaft, caudal to the insertion of M. latissimus dorsi (Gadow and Selenka, 1891; Fürbringer, 1902; Fisher, 1946; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; Schreiweis, 1982; McGowan, 1986; Vanden Berge and

Zweers, 1993). In most ratites, M. humerotriceps is reduced in volume (Fürbringer, 1888, 1902), but McGowan (1982) reported a substantial development of this muscle in *Apteryx*.

All heads of M. triceps brachii usually fuse in the distal part of the brachium and insert by a common tendon on the olecranon process of the ulna. In many forms, a sesamoid (the ulnar patella) is incorporated into this tendon. In some birds, M. scapulotriceps and M. humerotriceps insert at different points on this process (Hudson and Lanzilloti, 1955; McGowan, 1986).

DISCUSSION – The complex morphology of M. triceps brachii, with somewhat unclear homologies of the individual heads, hampers the inference of its morphology in the last common ancestor of birds and crocodilians. As mentioned above, Fürbringer (1876) noted that the scapular head has a different course in crocodilians. M. scapulotriceps of birds is similar in this respect, leading Fübringer (1886) to homologize both heads. To interpret the rugose scar immediately above the glenoid in basal archosaurs as the point of origin of the tendon of M. triceps brachii caput scapulare is therefore a Level I inference. On the other hand, Fürbringer (1886, 1888, 1902) found the avian M. coracotriceps to be homologous with the caput coracoideum of lepidosaurs, but not with the crocodilian caput coracoscapulare. According to Fürbringer, the latter head developed by fusion of the plesiomorphic caput coracoideum with a ventral division of caput scapulare, rendering the archosaurian caput scapulare in part a novel development, and caput coracoscapulare an autapomorphy of Crocodylia. However, basal archosaurs and dinosaurs have a slight eminence on the caudal edge of the scapular blade, which might be homologous to the rugose scar left by the insertion of the internal sternoscapular ligament in crocodilians (see chapter 4). Therefore, it cannot be ruled out that all archosaurus plesiomorphically had such a coracoscapular head of M. triceps brachii, which may have been secondarily lost in birds. Under consideration of the reorientation of the scapular blade and the general reduction of this head in birds, a loss of the scapular anchor would actually be expected. However, this interpretation is a Level II inference only.

Regarding the humeral parts of M. triceps brachii, it is obvious that birds have lost the lateral head, while they retained the medial head (caudal to the insertion of M. latissimus dorsi). Moreover, Fürbringer (1888, 1902) homologized the cranial part of the avian M. humerotriceps with the caput posticum of crocodilians. Some birds also exhibit a lateral head of M. humerotriceps in the craniodistal part of the brachium, but Fürbringer (1902) interpreted this as a convergent development. Since caput humerale laterale is a plesiomorphic feature that is retained in crocodylians, basal archosaurs may have possessed all three humeral heads of M. triceps brachii. Due to their fleshy origins, the exact extents of these heads are hard to delimit, unless clear intermuscular ridges are present. The common insertion of all heads on the olecranon process of the ulna is retained in all tetrapods. Therefore, it is a Level I inference to assume the same insertion in basal archosaurs.

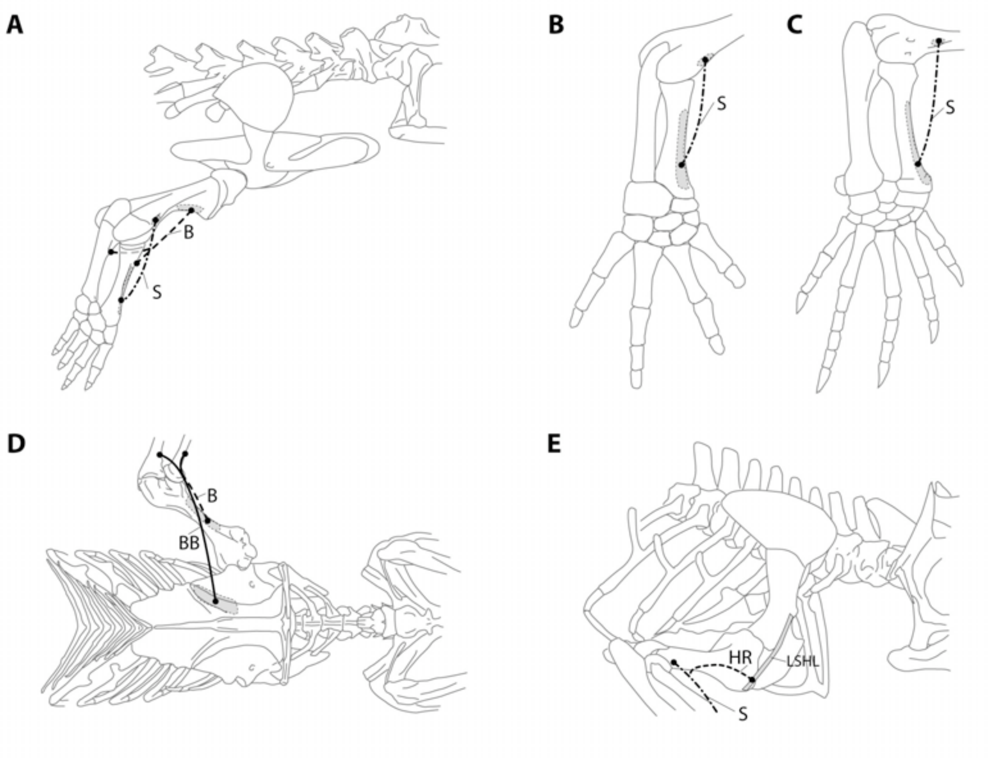

Figure 3-14. Proximal antebrachial musculature of urodeles (A, right lateral view; B, antebrachium in dorsal view) and *Sphenodon* (C, antebrachium in dorsal view; D, ventral view; E, right lateral view). Shaded lines of action indicate muscles that lie on the remote side of the respective bone.

18. M. biceps brachii (BB).

Synonyms:

M. biceps (MacAlister, 1864; Mivart, 1867, 1870; Sanders, 1870, 1872, 1874; de Vis, 1884; Rabl, 1916; Romer, 1922; Fisher, 1946; Fisher and Goodman, 1955; Walker, 1973; Dilkes, 2000)

M. biceps humeri (Haughton, 1866)

M. coraco-antebrachialis (Fürbringer, 1876; Byerly, 1925)

Remarks: For the same reasons as noted under 'M. triceps brachii', this thesis prefers to use the full term for this muscle instead of the common abbreviation 'M. biceps'. Fürbringer's (1876) alternative nomenclature did not prevail in the literature, and is therefore not taken into consideration.

DESCRIPTION – There is no M. biceps brachii in extant amphibians (Miner, 1925; Francis, 1934; Ribbing, 1938). Instead, its role of flexing the forearm is taken over by a specialized, deep part of M. supracoracoideus ('M. coracoradialis proprius'). The presence of M. biceps brachii (figs. 3-14, 3-15, 3-16) is a shared character of all amniotes. In *Sphenodon*, it arises fleshy from the medial part of the outer surface of the coracoid, and becomes tendinous in the region of the shoulder joint and deltopectoral crest. Distally the muscle again becomes fleshy, before it finally fuses close to the elbow joint to M. brachialis. It inserts via a forked tendon proximally on both the radius and the ulna (Fürbringer, 1900; Miner, 1925). Squamates exhibit a similar morphology, but in many forms the origin is somewhat more caudally placed (Mivart, 1867; Sanders, 1870, 1872, 1874; Fürbringer, 1876, 1900; Rabl, 1916). Chameleons and few other forms are specialized in having a tendinous origin of this muscle on the coracoid (Mivart, 1870; Fürbringer, 1876, 1900; de Vis, 1884). Moreover, Mivart (1870) observed that the radial tendon of M. biceps brachii in *Chamaeleo* leaves a prominent tubercle on the ulnar (medial) side of the radius. Romer (1922) stated that the ulnar as well as the radial insertion is associated with a rugose structure in most basal amniotes.

In turtles, M. biceps brachii has differentiated into two independent heads, a pars superficialis and a pars profundus. Both muscles arise from the caudal edge of the coracoid, the superficial part extending further medially than the deep head. Resembling lepidosaurs, the middle section of the superficial head is tendinous, while pars profundus partially fuses to M. brachialis. The superficial head inserts tendinously on the radius, while the deep head attaches by a tendon to the ulna (Walker, 1973). In contrast, crocodilians have a relatively weak, slim M. biceps brachii that arises by a wide, thin tendon from the cranioventral edge of the coracoid, cranially to M. coracobrachialis brevis (Fürbringer, 1876, 1900). At this location, it leaves a prominent, elongate scar that is oriented in parallel to the shaft axis (Cong et al., 1998; Meers, 2003). As in lepidosaurs, the muscle partly fuses to M. brachialis distally, and splits into two tendons that insert on the proximal ends of radius and ulna (Fürbringer, 1876, 1900; Ribbing, 1938). However, the radial insertion does not correlate to a tuberosity on the radius; instead, it is situated caudal to the prominent tubercle that serves as the anchor for the tendon of M. humeroradialis (Cong et al., 1998; Meers, 2003; Jasinoski et al., 2006; own observations).

The avian M. biceps brachii shows much variation. It is often reduced or differentiated into several small parts, including a pars propatagialis that controls the propatagial skin. In carinates, the muscle usually arises from the acrocoracoid process of the coracoid and the medial tuberosity of the humerus, both origins being connected by the Ligamentum acrocoracohumerale that spans over the dorsal side of the pectoral girdle (Fürbringer, 1902; Sy, 1936; Berger, 1966; Vanden Berge and Zweers, 1993). In some forms, the tendinous humeral origin extends distally beyond the medial tuberosity; in this case, a prominent bicipital crest is developed (McGowan, 1986; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955). M. biceps brachii arises tendinously, but becomes fleshy at the level of the deltopectoral crest. Like in other diapsids, it inserts by a forked tendon on both radius and ulna, where it correlates to tuberosities (Fürbringer, 1902; Berger, 1966; Vollmerhaus et al., 1992; Vanden Berge and Zweers, 1993). In ratites, the muscle has a relatively wide origin from the dorsolateral edge of the coracoid, immediately cranial to the glenoid. The ulnar insertion is weak in *Struthio* and missing in *Apteryx* (Fürbringer, 1902; McGowan, 1982).

DISCUSSION – Plesiomorphically, M. biceps brachii arises fleshy from the medial part of the external surface of the coracoid. Since the coracoids of both birds and crocodilians are strongly modified, and those of basal archosaurs are not, common characters of extant archosaurs (like a tendinous origin from the craniodorsal part of the coracoid) may indeed be due to convergence. Ostrom (1976) homologized the prominent tubercle present on the caudolateral side of dinosaurian coracoids with the avian acrocoracoid; therefore, the term 'biceps tubercle' for this structure is justified. Carpenter (2002) presented an alternative interpretation: he assumes that this protuberance is a remnant of bone between the large depressions for M. supracoracoideus and M. coracobrachialis, and did not serve for any muscle attachment. However, this tubercle is very large, quadrangular, and rugose in other dinosaurs (e.g., *Plateosaurus*, chapter 7), and has therefore clearly been associated with soft tissue in the living animal.

Since a humeral head of M. biceps brachii is present in most birds, but misses in crocodilians, its inference in basal archosaurs is equivocal. However, no basal archosaur exhibits a bicipital crest or a homologous structure next to the medial tuberosity that may correlate to the origin of a biceps tendon.

Regarding the insertion of M. biceps brachii, outgroup comparison clearly implies that a split tendon leading to both ulna and radius was present in basal archosaurs. The prominent tubercle on the cranial side of the radius is associated with M. biceps brachii in birds and some lepidosaurs, but with M. humeroradialis in crocodilians. Therefore, it is somewhat speculative to interpret such a structure in extinct archosaurs as the site of insertion of M. biceps brachii (chapter 5). If a tubercle is present cranially on the proximal ulna, it probably correlates to the insertion of the ulnar tendon of this muscle.

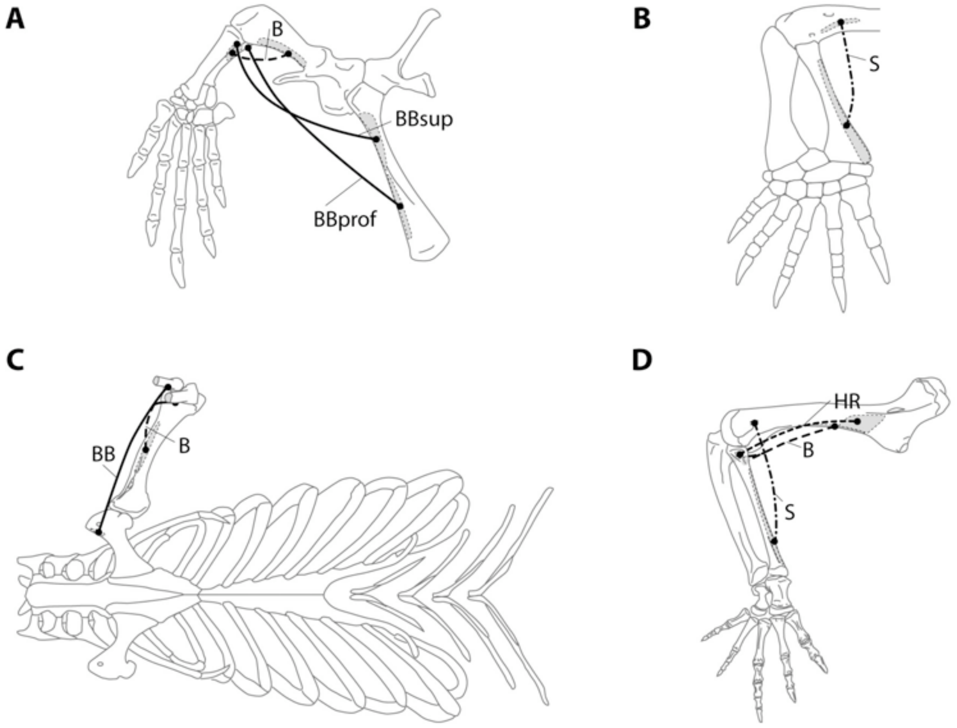

Figure 3-15. Proximal antebrachial musculature of chelonians (A, ventral view; B, antebrachium in dorsal view) and *Alligator* (C, ventral view; D, cranial view).

19. M. humeroradialis (HR).

Synonyms:

M. brachialis externus (Haughton, 1866)
M. brachio-radialis (Romer, 1922)
M. spiralis (Ribbing, 1938)
M. brachialis caput laterale (Cong et al., 1998)

Remarks: The term 'M. humeroradialis' was established by Fürbringer (1876), who recognized the unusual properties of this muscle. Many other workers regarded it as a specialized part of M. brachialis, or introduced own terminologies (e.g., 'M. brachio-radialis', Romer, 1922). However, recent workers on crocodilian myology use Fürbringer's terminology (Meers, 2003; Jasinoski et al., 2006). A homology of this muscle with the avian M. deltoideus propatagialis caput caudale is possible, but not proven.

DESCRIPTION – M. humeroradialis (figs. 3-14, 3-15) constitutes a remnant of a phylogenetically old muscle that has been lost in most extant diapsids. It is present in mammals (Romer, 1922; Ribbing, 1938), in *Sphenodon*, and in crocodilians. Romer (1944) observed its *anlage* also in embryos of *Lacerta*, but the muscle misses in any hatched squamate known. Some parts of M. deltoideus propatagialis of birds (see also above, 'M. deltoideus clavicularis') may also be homologous to M. humeroradialis (Fürbringer, 1876, 1900, 1902).

In *Sphenodon*, the muscle has no contact to the skeleton. It arises from the ventral end of Ligamentum scapulohumerale laterale, and from an aponeurosis that covers the caudal side of M. deltoideus clavicularis. Distally, it merges with the proximal parts of M. supinator (Fürbringer, 1900; Miner, 1925; Ribbing, 1938).

M. humeroradialis is well developed in crocodilians. Situated between M. brachialis and M. triceps brachii caput humerale laterale, it arises fleshy from the craniodorsal side of the humerus, just distal to M. deltoideus clavicularis (Haughton, 1866; Fürbringer, 1876, 1900; Meers, 2003; Jasinoski et al., 2006; own observation). Its area of origin is rugose in *Alligator,* and may also be clearly demarcated from the insertion of M. deltoideus clavicularis by a distinct scar (Meers, 2003). The muscle inserts via a strong tendon on the craniolateral side of the proximal radius, where it leaves a prominent tubercle (Fürbringer, 1876, 1900; Cong et al., 1998; Meers, 2003).

Fürbringer (1902) homologized parts of the avian M. deltoideus propatagialis caput breve with M. humeroradialis of *Sphenodon*. This avian muscle helps to span the propatagium and has no contact to the skeleton.

DISCUSSION – Based on their similar innervation, Fürbringer (1876) was the first to recognize the close relationship of M. deltoideus clavicularis and M. humeroradialis, a view later confirmed by Howell (1936) and Romer (1944). By now, it has not been convincingly shown that parts of the avian M. deltoideus propatagialis are homologous to the crocodilian M. humeroradialis. However, since the presence of this muscle seems to be a plesiomorphic trait of tetrapods, it probably existed also at the base of the archosaurs. Nevertheless, the muscle lacks a strong development or association with osteological correlates in any tetrapod group other than crocodilians. Therefore, postulating that structures visible on the humerus or radius of extinct archosaurs are traces of M. humeroradialis can only be a Level II inference. Some alternative configurations of the M. biceps brachii – M. humeroradialis – M. brachialis complex in sauropodomorphs will be discussed in the following chapters.

20. M. brachialis (B).

Synonyms:

- M. brachialis anticus (Haughton, 1866; Mivart, 1867, 1870; Sanders, 1870, 1872, 1874; de Vis, 1884)
- M. humero-antebrachialis inferior (Fürbringer, 1876; Byerly, 1925)

M. brachialis inferior (Gadow and Selenka, 1891; Fürbringer, 1888, 1900, 1902; Miner, 1925; Walker, 1973; Dilkes, 2000)

Remarks: Most authors used the term 'M. brachialis' for this muscle, but various epithets that describe its relative position on the arm were added. For standardization and simplification purposes, modern authors abandoned these epithets. Again, Fürbringer's (1876) alternative nomenclature did not find wide acceptance in the literature.

DESCRIPTION – Plesiomorphically, M. brachialis (figs. 3-14, 3-15, 3-16) is present in all amniotes and caudate amphibians. In the latter group, it has its origin on the proximal half of the humerus, just distal to the insertion of Mm. deltoidei ('M. procoracohumeralis superficialis', M. deltoideus scapularis). It inserts fleshy on the cranial proximal part of the radius (Miner, 1925; Walthall and Ashley-Ross, 2006). In *Sphenodon*, M. brachialis is strongly developed, and covers most of the cranioventral humeral shaft, beginning with the base of the deltopectoral crest. It has contact to M. humeroradialis dorsoproximally and merges with M. biceps brachii distally. Together with the latter muscle, M. brachialis inserts by a shared split tendon on both ulna and radius (Fürbringer, 1900; Miner, 1925). There is not much variation of this pattern in squamates, with the exception of the loss of M. humeroradialis (see above). This allows M. brachialis to have contact with the ventral part of M. triceps brachii caput humerale laterale (Mivart, 1867; Sanders, 1874; Fürbringer, 1876, 1900; de Vis, 1884; Rabl, 1916; Ribbing, 1938). Minor modifications found in chameleons and some other species include a reduction of the radial insertion, or an insertion independent from that of M. biceps brachii (Mivart, 1870; Sanders, 1870, 1872; Fürbringer, 1876, 1900). Turtles have a similar origin of this muscle, but the insertion is fleshy on the proximal third of the ulna and the adjacent radius (Walker, 1973).

In crocodilians, M. brachialis is relatively weak. Proximally, the muscle is in close connection with M. humeroradialis. It arises from the entire cranioventral humeral shaft distal to the deltopectoral crest, and fuses distally with M. biceps brachii, sharing the split tendon of insertion that runs to ulna and radius (see above, 'M. biceps brachii'). In some species, the ulnar insertion is reduced (Haughton, 1866; Fürbringer, 1876, 1900; Ribbing, 1938; Cong et al., 1998; Meers, 2003).

The avian M. brachialis is short and restricted to the elbow region. As in turtles, both origin and insertion are fleshy. The muscle arises from the distal part of the humeral shaft, just proximal to the entepicondyle, where it is associated with a slight depression (Fürbringer, 1888, 1902; Gadow and Selenka, 1891; Hudson and Lanzilloti, 1955, 1964; Vollmerhaus et al., 1992). It inserts obliquely on the proximoventral (developmentally medial) surface of the ulna, where it correlates to a depression at least in some forms (McGowan, 1982, 1986; Fisher, 1946; Fisher and Goodman, 1955; Berger, 1966). An additional radial insertion is present in *Struthio, Apteryx* and penguins (Fürbringer, 1888, 1902; McGowan, 1982; Schreiweis, 1982).

DISCUSSION – M. brachialis shows little variation in its relative position, but some modifications in its extent and point of insertion. In basal amniotes, the humeral shaft exhibits four triangular facets, one of these being probably associated with M. brachialis (Romer, 1922). However, such facets are not distinguishable in archosaurs any more, making the exact extend of the origin of M. brachialis in fossil archosaurs hard to delimit. Nevertheless, phylogenetic inference implies that the muscle arose from the humeral shaft distal to the deltopectoral crest in basal archosaurs, and that it inserted together with M. biceps brachii on both radius and ulna in these forms. The separate insertion of both muscles is a derived character probably restricted to Aves, because the osteological correlates of M. brachialis found in birds are still missing in their closest outgroup, the Dromaeosauridae (Jasinoski et al., 2006).

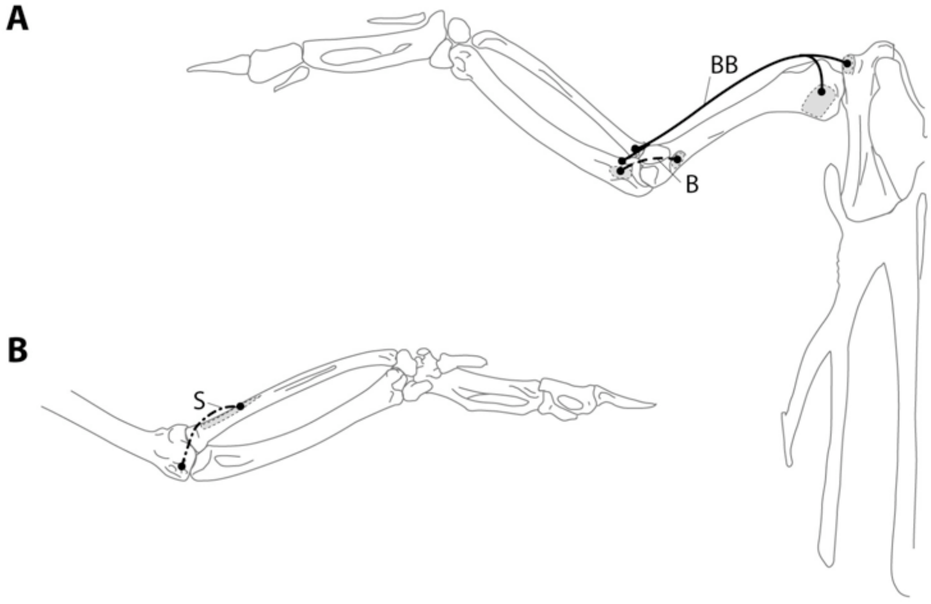

Figure 3-16. Proximal antebrachial musculature of *Gallus* (A, ventral view; B, dorsal view).

21. M. supinator (S).

Synonyms:

M. ectepicondylo-radialis (Gadow and Selenka, 1891)
M. extensor antebrachii radialis *partim* (Ribbing, 1907, 1938)
M. abductor antebrachii radialis (Rabl, 1916)
M. extensor carpi radialis *partim* (Byerly, 1925; Dilkes, 2000; Abdala and Moro, 2006)
M. tractor radii (Haines, 1939; Walker, 1973)
M. brachioradialis (Haines, 1939)

Remarks: The nomenclature of the forearm musculature of tetrapods is confused, because many late 19th and early 20th century authors grouped the individual muscle heads that arise from the humeral epicondyles differently under various names, in most cases without testing their homologies (see also the note on the antebrachial extensor musculature below). Therefore, this thesis prefers the most recent nomenclatorial system of Meers (2003), but replaces some of his new terms by NAA standardized terminology (Vanden Berge and Zweers, 1993). In case of M. supinator, both Meers (2003) and the NAA prefer this classical term to the alternatives listed above.

DESCRIPTION – M. supinator (figs. 3-14, 3-15, 3-16) is part of the antebrachial extensor musculature that arises from the ectepicondylar region of the humerus. It can be distinguished from other muscles of that group by its extensive, fleshy insertion on the craniomedial side of the radius. M. supinator therefore serves to rotate the hand outwards.

In caudatans, the muscle has a tendinous origin from the lateral side of the ectepicondyle, and inserts fleshy on the distal part of the craniomedial radius (Miner, 1925). Some forms exhibit no clear distinction of this muscle from M. extensor carpi radialis and M. abductor radialis (Ribbing, 1907; Walthall and Ashley-Ross, 2006).

In *Sphenodon* and other lepidosaurs, the muscle arises from the proximal part of the ectepicondyle, the other extensor muscles being situated more distal. The origin correlates to the supinator crest, a remnant of the prominent supinator process of early tetrapods (Romer, 1922; Miner, 1925). M. supinator inserts fleshy along the craniomedial side of the radius (Mivart, 1867, 1870; Sanders, 1870, 1872, 1874; de Vis, 1884; Ribbing, 1907, 1938; Rabl, 1916; Byerly, 1925; Miner, 1925; Haines, 1939; Abdala and Moro, 2006).

The chelonian M. supinator is specialized by having an extended, fleshy origin that covers the ventral part of the distal third of the humerus. As in other nonavian Reptilia, it inserts onto the entire craniomedial side of the radius (Ribbing, 1938; Walker, 1973). In crocodilians, the morphology is generally very similar to that of lepidosaurs: The muscle arises by a tendon from the ectepicondyle close to M. extensor carpi radialis, and inserts fleshy along the craniomedial radial shaft, distal to the tubercle for the insertion of M. humeroradialis (Ribbing, 1907, 1938; Cong et al., 1998; Meers, 2003).

In birds, M. supinator is a short muscle that spans over the elbow joint. It arises tendinously, together with M. extensor digitorum communis, from the craniolateral ectepicondyle, and inserts fleshy within the proximodorsal half of the radius, distal to the biceps tubercle (Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; Schreiweis, 1982; McGowan, 1986; Vollmerhaus et al., 1992; Vanden Berge and Zweers, 1993). In ratites, its insertion may extend along the entire shaft of the radius (MacAlister, 1864; Gadow and Selenka, 1891; McGowan, 1982).

DISCUSSION – M. supinator is relatively conservative: In most tetrapods, it arises tendinously from the proximal ectepicondyle, and inserts fleshy on the craniomedial shaft of the radius. This is also true for crocodilians and birds; however, the extent of the insertion is somewhat reduced in neognaths. It is therefore a level I inference to reconstruct a M. supinator with a similar origin and insertion in basal archosaurs.

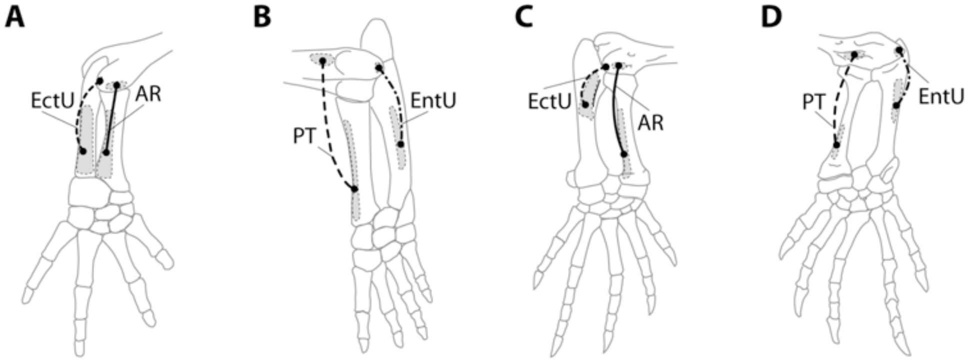

Figure 3-17. Antebrachial muscles arising from the epicondyles in urodeles (A, dorsal view; B, ventral view) and *Sphenodon* (C, dorsal view; D, ventral view).

22. M. abductor radialis (AR).

Synonyms:

- M. supinator longus *partim* (Mivart, 1867, 1870)
- M. supinator brevis (Sanders, 1870)
- M. extensor longus digitorum *partim* (Sanders, 1872, 1874)
- M. extensor antebrachii et carpi radialis *partim* (Ribbing, 1907; Walthall and Ashley-Ross, 2006)
- M. extensor carpi radialis b (Ribbing, 1907)

M. abductor antibrachii radialis *partim* (Rabl, 1916)

M. extensor carpi radialis *partim* (Byerly, 1925; Dilkes, 2000; Abdala and Moro, 2006)

M. extensor carpi radialis profundus (Miner, 1925)

M. extensor radialis profundus (Haines, 1939; Walker, 1973)

Remarks: Being a part of the antebrachial extensor musculature, the nomenclatorial confusion mentioned in the last paragraph also pertains to M. abductor radialis. Since this muscle is lost in birds and no NAA term is available, it is regarded here as best solution to adopt the term recently introduced by Meers (2003), M. abductor radialis.

DESCRIPTION – Like M. supinator, M. abductor radialis (figs. 3-17, 3-18) differentiated from the primordial extensor mass found in amphibians, M. extensor antebrachii et carpi radialis. The amphibian muscle arises by a short tendon from the distal part of the ectepicondyle and inserts on the entire cranial side of the radius, the radiale, and the intermedium (Ribbing, 1907; Miner, 1925; Walthall and Ashley-Ross, 2006). However, Haines (1939) found an internal differentiation of this muscle into a M. supinator, M. abductor radialis, and M. extensor carpi radialis in *Salamandra* (see the sections on these muscles for his synonyms).

In *Sphenodon*, squamates, chelonians, and crocodilians, M. abductor radialis takes origin from the ventrodistal part of the ectepicondyle. It inserts on almost the entire craniolateral face of the radius, beginning just distal to the insertion of M. biceps brachii (Mivart, 1867; Sanders, 1870, 1872; Ribbing, 1907; Rabl, 1916; Byerly, 1925; Miner, 1925; Haines, 1939; Walker, 1973; Abdala and Moro, 2006). The area of insertion is restricted to about the proximal half of the radius in crocodilians, and may vary in some squamates (Mivart, 1870; Sanders, 1874; Ribbing, 1907; Meers, 2003).

There is no equivalent muscle in extant birds.

DISCUSSION – This plesiomorphic muscle, which is present in all lepidosaurs and turtles, is preserved in modern day crocodilians, albeit somewhat reduced in length. Consequently, it is probable that M. abductor radialis was also present in basal archosaurs and arose by a tendon from the ectepicondyle. However, its fleshy type of insertion without unambiguous osteological correlates does not allow for an exact delimitation of its extent. Since birds have lost this muscle, its reconstruction in sauropodomorphs is merely a level II inference in terms of Witmer (1995). Nevertheless, the retention of this muscle in different types of amniotes implies that its loss in birds is correlated to the evolution of flight, and that it was reduced only late in dinosaur evolution.

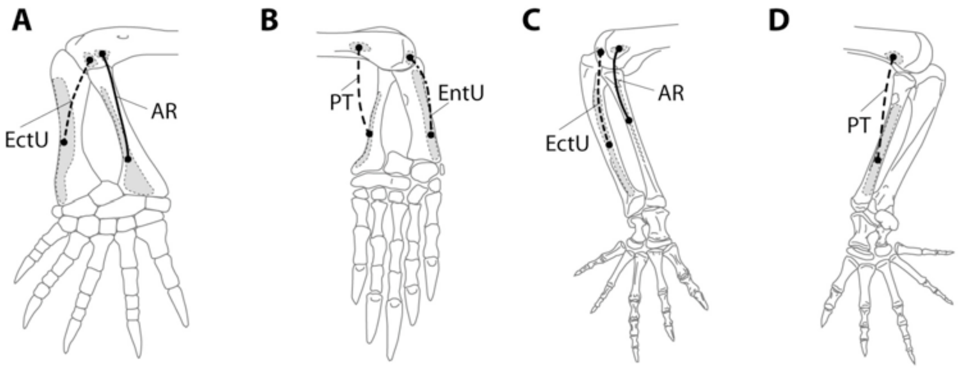

Figure 3-18. Antebrachial muscles arising from the epicondyles in chelonians (A, dorsal view; B, ventral view) and *Alligator* (C, dorsal view; D, ventral view).

23. M. ectepicondylo-ulnaris (EctU).

Synonyms:

M. anconaeus (Haughton, 1866; Fisher, 1946; Fisher and Goodman, 1955; Berger, 1953, 1954, 1955, 1956a–c, 1957, 1960, 1966; Hudson and Lanzilloti, 1955, 1964)
M. extensor antebrachii ulnaris (Ribbing, 1907, 1938; Haines, 1939)
M. extensor ulnaris (Romer, 1922; Haines, 1939)
M. anconaeus quartus (Miner, 1925)
M. extensor carpi ulnaris (Cong et al., 1998)
M. flexor ulnaris (Meers, 2003)
M. extensor antebrachii et carpi ulnaris (Walthall and Ashley-Ross, 2006)

Remarks: This muscle has long been referred to as ‘M. anconaeus’ in the ornithological literature. However, this term also has been used as a synonym for M. triceps (e.g., Fürbringer, 1876), and has therefore been replaced by ‘M. ectepicondylo-ulnaris’ in the NAA to avoid confusion. Due to the lack of a widely accepted nomenclatorial system for the forearm musculature of non-avian Reptilia, the homologous muscle of these forms bears various names. Since the orientation of this muscle is same in all diapsids, and the NAA term is descriptive (rather than based on function, which is subject to change throughout evolution), it is here considered best to apply this term throughout this work.

DESCRIPTION – M. ectepicondylo-ulnaris (figs. 3-17, 3-18, 3-19) is plesiomorphically present in all tetrapods, but lost in squamates. It is closely related to M. extensor carpi ulnaris; both muscles are fused in some amphibians and turtles. In these forms, M. ectepicondylo-ulnaris has its tendinous origin on the distal-most point of the ectepicondyle, and inserts fleshy along the lateral side of the ulnar shaft, the ulnare, and the pisiforme. In chelonians, the insertion extends onto metacarpal V (Ribbing, 1907, 1938; Haines, 1939; Walker, 1973; Walthall and Ashley-Ross, 2006). The more distal parts of this muscle mass must be regarded as homologues of M. extensor carpi ulnaris, and will be treated later. A full differentiation into two independent muscles is found in anurans and in *Salamandra* (Ribbing, 1938; Haines, 1939).

In *Sphenodon*, the common muscular body has differentiated into two distinct parts. M. ectepicondylo-ulnaris exhibits the same general topology as in more basal tetrapods, but its insertion is restricted to the proximal half of the ulnar shaft (Miner, 1925; Ribbing, 1938; Haines, 1939). The muscle is completely lost in squamates.

Crocodilians have reduced the carpal part of this muscle complex (see below, 'M. extensor carpi ulnaris'). The remaining M. ectepicondylo-ulnaris attaches to the lateral side of the entire shaft of the ulna (Haughton, 1866; Ribbing, 1907, 1938; Cong et al., 1998; Meers, 2003).

In contrast to squamates and crocodilians, birds kept both M. ectepicondylo-ulnaris and M. extensor carpi ulnaris (= 'M. extensor metacarpi ulnaris' in NAA terminology). As in other tetrapods, M. ectepicondylo-ulnaris takes origin by a strong tendon from the distal ectepicondyle. The muscle inserts dorsocranially (developmentally craniolaterally) on the proximal half of the ulnar shaft, in some forms (e.g., galliforms) on the entire ulnar shaft (Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; McGowan, 1982, 1986; Schreiweis, 1982; Vollmerhaus et al., 1992). It is partly fused to M. extensor metacarpi ulnaris in *Struthio* (Gadow and Selenka, 1891).

DISCUSSION – M. ectepicondylo-ulnaris is present in both crocodilians and birds and has a conservative course. Therefore, it is easy to infere its presence in basal archosaurs. Moreover, in all tetrapods M. ectepicondylo-ulnaris is the distalmost of the ectepicondylar muscles. However, some speculation is required regarding the extent of its insertion, since there are no clear osteological correlates. Nevertheless, both in crocodilians and in plesiomorphic birds such as galliforms, the muscle covers the complete lateral side of the shaft of the ulna, rendering a similar pattern in basal archosaurs probable.

24. M. pronator teres (PT).

Synonyms:

M. pronator radii (Haughton, 1866; Sanders, 1872, 1874)
M. entepicondylo-radialis (Gadow and Selenka, 1891)
M. flexor antebrachii radialis (Ribbing, 1907)
M. pronator radii teres (Miner, 1925)
M. pronator brevis, M. pronator longus (Fisher, 1946; Fisher and Goodman, 1955; Fujioka, 1959)

M. pronator sublimis (Hudson and Lanzilloti, 1955, 1964)

M. pronator superficialis, M. pronator profundus (Vanden Berge and Zweers, 1993, and other ornithological literature)

Remarks: Most authors use the originally mammalian term ‘M. pronator teres’ for this muscle. In birds, both pronators (M. pronator superficialis, M. pronator profundus = ‘M. pronator brevis’, ‘M. pronator longus’) seem to be derived from this muscle (Sullivan, 1962). Therefore, the mammalian terms M. pronator teres and M. pronator quadratus are adapted throughout this thesis to avoid confusion. Ribbing (1907) suggested an alternative nomenclature, and grouped M. pronator teres (his ‘M. flexor antebrachii radialis’) together with M. flexor carpi radialis. He further interpreted M. pronator accessorius of squamates as the true homologue of the mammalian M. pronator teres, and claimed the chelonian M. pronator teres to be a homologue of this latter muscle. Consequently, this led him to report that ‘M. flexor antebrachii radialis’ is lost in turtles. However, most other authors correctly identified M. pronator teres throughout the various tetrapod groups, and recognized the small, additional pronator of squamates as an autapomorphic trait, probably derived from M. pronator quadratus (see below, ‘M. pronator quadratus’).

DESCRIPTION – The presence of an independent M. pronator teres (figs. 3-17, 3-18, 3-19) is a synapomorphic character of amniotes. In modern amphibians, the fibers that arise from the entepicondyle and insert onto the radial shaft are still part of a larger muscle called ‘M. flexor antebrachii et carpi radialis’ (Walthall and Ashley-Ross, 2006). Alternatively, Miner (1925) suggested that some fibers of the amphibian M. flexor digitorum communis might be homologous to M. pronator teres.

In all diapsids, M. pronator teres arises tendinously from the entepicondyle. In lepidosaurs, its origin is often located on the summit of the entepicondylar region. The muscle inserts fleshy on the cranial radial shaft in interspecifically varying positions, sometimes medially, sometimes laterally, more proximally, more distally, or along the entire shaft (Mivart, 1867, 1870; Sanders, 1872, 1874; Ribbing, 1907, 1938; Rabl, 1916; Byerly, 1925; Miner, 1925; Haines, 1950; Abdala and Moro, 2006). Essentially the same changing conditions are found in turtles (Ribbing, 1907, 1938; Walker, 1973) and crocodilians (Haughton, 1866; Ribbing, 1907, 1938; Cong et al., 1998; Meers, 2003). However, a constant character of this muscle is that its area of insertion is always situated distal to the insertions of M. humeroradialis, M. biceps brachii, and M. brachialis.

The superficial portion of M. pronator teres (M. pronator superficialis) did not change much in birds. In *Apteryx*, the tendon of origin is shared with M. flexor carpi ulnaris (McGowan, 1982; = ‘M. flexor metacarpi ulnaris’), but in most birds, the tendon arises autonomously from the proximal part of the entepicondyle. The insertion is in most cases fleshy on the ventral (developmentally cranial) side of the shaft of the radius, again in varying relative lengths and positions (MacAlister, 1864; Gadow and Selenka, 1891; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; McGowan, 1982, 1986; Vollmerhaus et al., 1992).

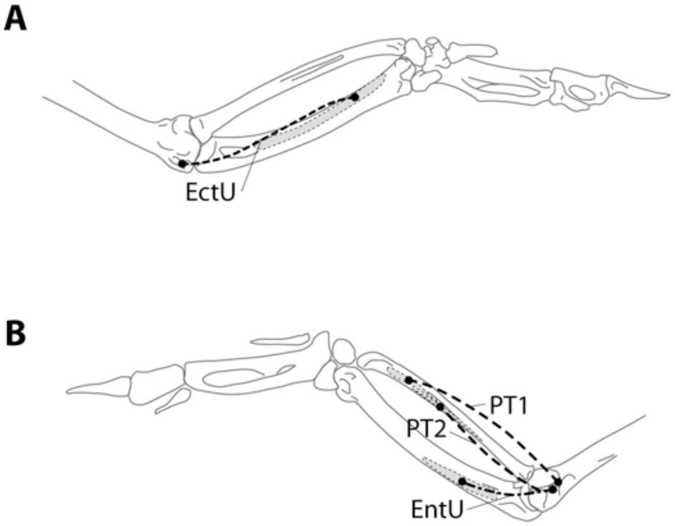

Figure 3-19. Antebrachial musculature arising from the epicondyles in *Gallus* (A, dorsal view; B, ventral view).

The avian 'M. pronator profundus' arises distally from the entepicondyle, but shares its tendon of origin with M. entepicondylo-ulnaris. The origin is located between that of 'M. pronator superficialis' and that of a derivate of M. flexor digitorum longus, 'M. flexor digitorum superficialis'. The muscle inserts fleshy along a narrow line on the caudoventral side of the radius, caudally to 'M. pronator superficialis'. The length and position of this insertion on the radial shaft is variable (Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Bentz, 1979; McGowan, 1986; Vanden Berge and Zweers, 1993). Both pronators, 'M. pronator superficialis' and 'M. pronator profundus', are fused in ratites (Gadow and Selenka, 1891; Berger, 1966; McGowan, 1982).

DISCUSSION – M. pronator teres is present in all diapsids and has a fairly constant position. It always arises from the entepicondylar region and inserts on the cranial part of the radial shaft. Therefore, it can be concluded that basal archosaurs had a M. pronator teres in a similar position (Level I inference). However, the exact extent of the area of insertion of this muscle on the radius is in most cases hard to delimit, since the fleshy insertion usually is not associated with osteological correlates. The differentiation of M. pronator teres into two largely independent muscles probably is autapomorphic for Neornithes.

25. M. entepicondylo-ulnaris (EntU).

Synonyms:

M. supinator accessorius (Mivart, 1867)
M. supinator brevis (de Vis, 1884)
M. flexor antebrachii ulnaris (Ribbing, 1907, 1938)
M. anconeus medialis (Fujioka, 1959)
M. epitrochleo-anconaeus (Miner, 1925; Haines, 1950)
M. epitrochleoanconeus (Abdala and Moro, 2006)
'gallinaceous muscle' (ornithological literature)

Remarks: This muscle has received various names, and in many myological descriptions it was overlooked. When mentioned, the name used for this muscle was either based on mammalian anatomy (M. epitrochleo-anconaeus) or on the system of Ribbing (1907), or a new name was introduced. Since there is no general agreement over the nomenclature of this muscle, it is here considered best to use the standardized term of the NAA (Vanden Berge and Zweers, 1993), M. entepicondylo-ulnaris. This term is descriptive and, because of the conservative nature of this muscle, also applicable to other diapsids.

DESCRIPTION – The presence of M. entepicondylo-ulnaris (figs. 3-17, 3-18, 3-19) is a plesiomorphic character of tetrapods. It constantly arises from the entepicondyle, sometimes sharing its tendon of origin with M. flexor carpi ulnaris, and attaches fleshy to the medial side of the ulna. The area of insertion varies within groups and species. In some caudatans, the muscle is lost (Ribbing, 1907) or fused to M. flexor carpi ulnaris (Walthall and Ashley-Ross, 2006), but it normally inserts on the middle of the shaft of the ulna (Ribbing, 1907; Miner, 1925). In lepidosaurs, M. entepicondylo-ulnaris inserts variably on the medial side of the ulna, but normally attaches within the proximal half of that bone (Mivart, 1867; de Vis, 1884; Ribbing, 1907, 1938; Rabl, 1916; Miner, 1925; Haines, 1950; Abdala and Moro, 2006). The muscle seems to be fused to M. flexor carpi ulnaris in *Chamaeleo* (Mivart, 1870).

In chelonians, the area of insertion of M. entepicondylo-ulnaris is extended along the entire medial side of the ulna. In most forms, the muscle has fused to M. flexor carpi ulnaris, or the partition of both muscles is indistinct (Ribbing, 1907, 1938; Walker, 1973). Crocodilians have completely lost M. entepiconylo-ulnaris (Ribbing, 1907).

In birds, the muscle is preserved only in Galloanserae and tinamous (Hudson et al., 1972). Berger (1966) and Vanden Berge and Zweers (1993) reported its presence in the kiwi, but McGowan (1982) found the muscle to be absent in his sample. M. entepicondylo-ulnaris has not been identified in other palaeognaths. When present, it arises together with M. pronator profundus (see above, 'M. pronator teres') from the craniodistal corner of the entepicondyle, and has a fleshy insertion on the caudoventral (developmentally medial) side of the shaft of the proximal ulna, between the insertion of M. brachialis and the origin of 'M. ulnometacarpalis ventralis' (= M. pronator quadratus) (Gadow and Selenka, 1891; Berger, 1966; Sullivan, 1962; Hudson and Lanzilloti, 1964; Vollmerhaus et al., 1992; Vanden Berge and Zweers, 1993).

DISCUSSION – M. entepicondylo-ulnaris is present in most tetrapods, including basal birds. Its absence in flightless palaeognaths might be secondary. Although the muscle is lost in crocodilians, it is hence probable that it was still present at the base of the archosaurs. Strict application of the EPB without considering the outgroups would provide only equivocal or even contrary results, depending on which sample taxa are chosen for Aves. Romer (1922) reported this muscle to have osteological correlates on the ulnae of early amniotes, but in fossil archosaurs the extent of its insertion is usually hard to delimit.

26. M. pronator quadratus (PQ).

Synonyms:

M. ulni-metacarpalis ventralis (Gadow and Selenka, 1891)
M. pronator profundus, M. interosseus antebrachii (Ribbing, 1907, 1938)
M. pronator profundus (Rabl, 1916; Haines, 1950; Cong et al., 1998)
M. flexor carpi ulnaris brevis (Fisher, 1946; Fisher and Goodman, 1955; Berger, 1966)
M. ulnometacarpalis ventralis (Vanden Berge and Zweers, 1993, and other ornithological literature)

Remarks: The term used throughout this thesis and in many other works, 'M. pronator quadratus', is based on the form of this muscle in mammals. In Reptilia, the muscle is often not quadrangular, leading some authors to prefer the term 'M. pronator profundus', but this would cause confusion with the avian muscle of the same name (see above, 'M. pronator teres'). The amphibian 'M. pronator profundus' listed by Ribbing (1907, 1938) actually refers to M. ulnocarpalis, a muscle lost in amniotes. Ribbing (1907) correctly uses M. pronator profundus for the other tetrapod groups, but names the amphibian homologue 'M. interosseus antebrachii'. In birds, the muscle is called 'M. ulnometacarpalis ventralis' by most authors. 'M. ulnometacarpalis dorsalis' is derived from the Mm. extensores digitorum superficiales system and not related to M. pronator quadratus (Sullivan, 1962; see below, 'Mm. extensores digitorum superficales').

DESCRIPTION – M. pronator quadratus (figs. 3-20, 3-21, 3-22) is present in most tetrapods, with the exception of anurans (Ribbing, 1907, 1938). The caudatan M. pronator quadratus arises fleshy from the entire lateral side of the shaft of the ulna and inserts on the opposing side of the shaft of the radius, as well as on the ventral (flexor) surfaces of the radial and first carpal (Ribbing, 1907; Miner, 1925). In some forms, the origin extends onto the ulnare and intermedium, while the insertion is restricted to the carpus (Walthall and Ashley-Ross, 2006).

In *Sphenodon*, the muscle has its origin on the radial side of the shaft of the ulna. The same is the case in other lepidosaurs, but occasionally the origin is located on the distal ulna only. M. pronator quadratus usually inserts on the distal half of the radius and on the radiale, but may extend onto the whole shaft of the radius in some forms (Mivart, 1867, 1870; Sanders, 1870; de Vis, 1884; Ribbing, 1907, 1938; Rabl, 1916; Byerly, 1925; Miner, 1925; Haines, 1950; Abdala and Moro, 2006). Additionally, squamates have a second pronator (M. pronator accessorius) that arises from the entepicondyle and inserts fleshy on the proximal radius. Since this muscle is often coadunate with M. pronator quadratus, Ribbing (1907, 1938) suggested that it may be a specialized part of the latter muscle.

The insertion of M. pronator quadratus on the radius is lost in turtles, restricting the attachment of this muscle to the lateral carpus and to the base of the first metacarpal (Ribbing, 1907, 1938; Walker, 1973). In comparison, the pattern found in crocodilians resembles *Sphenodon*: M. pronator quadratus covers most of the radial side of the ulna and the ulnar side of the radius, but there is no insertion on the radiale (Haughton, 1866; Ribbing, 1907, 1938; Cong et al., 1998; Meers, 2003).

The avian 'M. ulnometacarpalis ventralis' usually arises ventrally from the ulnar shaft. The origin may vary in relative length and position, but is located on the distal half of the ulna in many birds. The tendon of insertion wraps around the ventral side of the radiale and inserts craniodorsally on the carpometacarpus, directly proximal to the base of metacarpal I (Gadow and Selenka, 1891; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Berger, 1966; McGowan, 1986; Vollmerhaus et al., 1992; Vanden Berge and Zweers, 1993). Because of similarities in development and position, Sullivan (1962) homologized this muscle with M. pronator quadratus of other amniotes.

DISCUSSION – The insertion of M. pronator quadratus on the shaft of the radius is a plesiomorphic character of amniotes. This connection is lost only in turtles and birds, whereas in crocodilians it is extensive. Strict phylogenetic inference leaves it unresolved whether the muscle in basal archosaurs inserted on the radius, on the carpus, or on both. However, under consideration of the outgroups, it seems probable that the insertion on the radius was retained in these forms. Alternatively, the connection to the radius may have been already lost in the last common ancestor of birds, crocodilians, and turtles, rendering the crocodilian condition a reversal. In any way, the fleshy origin and insertion, usually without clear osteological correlates, make it difficult to reconstruct the extent of this muscle.

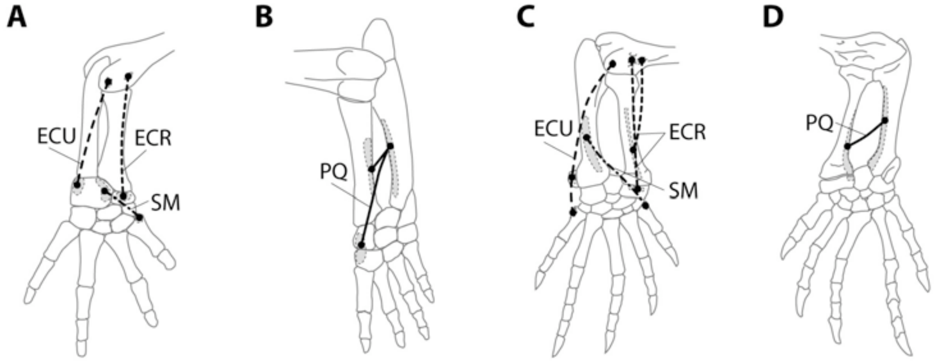

Figure 3-20. M. pronator quadratus and extensor muscles acting on the carpus of urodeles (A, dorsal view; B, ventral view) and *Sphenodon* (C, dorsal view; D, ventral view).

IV. Manual muscles.

As a convention, avian digits will be addressed here as I, II, and III, following Vargas and Fallon (2005a,b).

a) Antebrachial musculature acting on the hand

Note: There is particularly little compatibility between the muscles of the avian forearm extensor mass and those of other tetrapods. In this thesis, a set of homologies is used that is regarded as most parsimonious by the author. The arguments for this choice are discussed in the following. However, there is little, if any, positive evidence for these homologies, since both topology and innervation patterns are ambiguous. Therefore, the homologies suggested here should be tested by future research, especially by means of developmental and genetic examinations.

27. M. extensor carpi radialis (ECR).

Synonyms:

- M. extensor antebrachii et carpi radialis *partim* (Ribbing, 1907, 1938; Walthall and Ashley-Ross, 2006)
- M. extensor carpi radialis superficialis (Miner, 1925)
- M. extensor radialis superficialis, M. extensor radialis intermedius (Haines, 1939)
- M. extensor carpi radialis longus (Fujioka, 1959)
- M. extensor metacarpi radialis (Fisher, 1946; Berger, 1953, 1954, 1955, 1956a–c, 1957, 1960, 1966; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Sullivan, 1962; McGowan, 1982, 1986; Schreiweis, 1982)
- M. extensor carpi radialis longus (Meers, 2003)
- M. extensor carpi radialis intermedia (Abdala and Moro, 2006)

Remarks: The term 'M. extensor carpi radialis' is often used in a wider context, subsuming other muscles like M. abductor radialis or M. supinator (e.g., in Ribbing, 1907). Here, it is restricted to the muscle that connects the ectepicondyle and the dorsomedial carpus, listed as 'M. extensor carpi radialis pars superficialis' and 'pars intermedius' in Haines (1939). Both heads are treated together, since they show tendencies to fuse in some groups (e.g., turtles) and probably have a common phylogenetic origin.

DESCRIPTION – M. extensor carpi radialis (figs. 3-20, 3-21, 3-22) is part of the antebrachial extensor complex that arises by several tendons from the ectepicondyle of the humerus. In amphibians, it is still part of an undivided muscle mass (M. extensor antebrachii et carpi radialis) and inserts on the dorsal side of the radiale, sometimes also extending its insertion onto the ulnare, centrale, or intermedium (Ribbing, 1907, 1938; Miner, 1925; Haines, 1939).

The beginning differentiation of this muscle mass observed in some amphibians (Miner, 1925) is complete in amniotes. In lepidosaurs plesiomorphically, the central part has a tendinous origin on the central ectepicondyle, and consists of two distinct muscle heads that insert on the dorsal side of the radiale and on the cranial face of the radius, between M. abductor radialis and M. supinator (Sanders, 1870; Ribbing, 1907, 1938; Byerly, 1925; Haines, 1939; Abdala and Moro, 2006). The former part is named pars superficialis, the latter pars intermedius. These two muscles are often lost in squamates (Mivart, 1867, 1870; Sanders, 1872, 1874; de Vis, 1884; Rabl, 1916). Turtles exhibit the same pattern, but pars superficialis and pars intermedius are fused in some species (Ribbing, 1907, 1938; Haines, 1939; Walker, 1973).

Crocodilians differ only by having lost pars intermedius. The remaining M. extensor carpi radialis inserts via a tendon proximomedially on the radiale (Ribbing, 1907, 1938; Haines, 1939; Meers, 2003; own observation). A similar pattern is found in birds: M. extensor carpi radialis arises by a tendon cranially from the ectepicondyle, passes the radiale dorsally, and inserts on the extensor process of the carpometacarpus near the base of metacarpal I (Hudson and Lanzilloti, 1955, 1964; Fujioka, 1959; Berger, 1966; Sullivan, 1962; McGowan, 1982; Schreiweis, 1982; Vollmerhaus et al., 1992). In some forms, the muscle may be subdivided into two heads (Fisher, 1946; Fisher and Goodman, 1955; McGowan, 1986; Vanden Berge and Zweers, 1993).

DISCUSSION – A tendinous origin on the ectepicondyle is a constant character of M. extensor carpi radialis in all Reptilia. The loss of this muscle in several squamates is an autapomorphic trait, as well as the somewhat more distal insertion on a newly developed osteological correlate (the carpometacarpal extensor process) in birds. It is therefore probable that in basal archosaurs the muscle inserted via a tendon on the radiale. Phylogenetic inference implies that the head inserting on the radius (M. extensor carpi radialis intermedius) was lost at the root of the archosaurs. Since this head usually does not leave osteological traces, there are no clues to argue for the opposite.

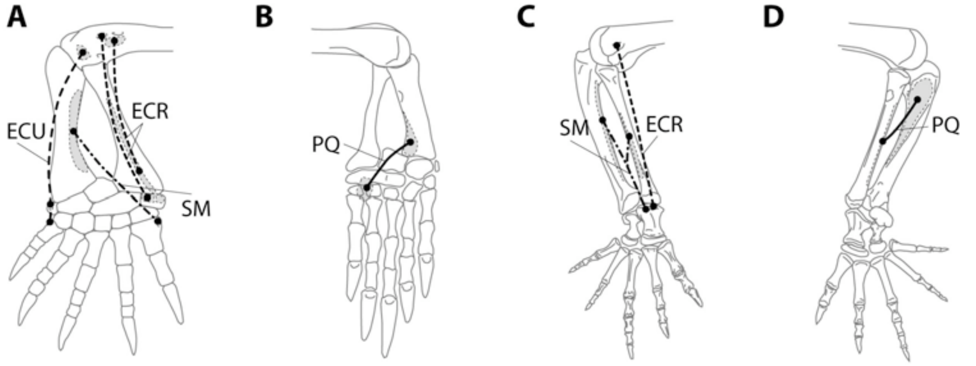

Figure 3-21. M. pronator quadratus and extensor muscles acting on the carpus of chelonians (A, dorsal view; B, ventral view) and *Alligator* (C, dorsal view; D, ventral view).

28. M. extensor carpi ulnaris (ECU).

Synonyms:

M. extensor metacarpi ulnaris (Gadow and Selenka, 1891; Sullivan, 1962; Berger, 1966; Vanden Berge, 1979; McGowan, 1982, 1986; Schreiweis, 1982)

M. extensor antebrachii et carpi ulnaris *partim* (Ribbing, 1907, 1938; Walthall and Ashley-Ross, 2006)

'ulnar extensor' *partim* (Romer, 1922)

M. flexor metacarpi radialis (Fisher, 1946; Fisher and Goodman, 1955)

Remarks: Most authors referred to the most caudal muscle of the forearm as M. extensor carpi ulnaris. Meers (2003) did not recognize that the muscle is lost in crocodilians and therefore misleadingly identified M. extensor digitorum communis as 'M. extensor carpi ulnaris longus'. Some ornithological works name this muscle 'M. extensor metacarpi ulnaris', but this alternative was abandoned in the NAA (Vanden Berge and Zweers, 1993). Few authors used the synonym 'M. flexor metacarpi radialis', because functionally the muscle is a flexor. However, Sullivan (1962) demonstrated its derivation from the extensor mass, and recommended to use the common term.

DESCRIPTION – In many urodele amphibians, M. extensor carpi ulnaris (figs. 3-20, 3-21, 3-22) has not yet fully differentiated from M. ectepicondylo-ulnaris (see also section 'M. ectepicondylo-ulnaris' above). The common muscle mass is usually called M. extensor antebrachii et carpi ulnaris (Ribbing, 1907; Walthall and Ashley-Ross, 2006). It arises together with M. extensor digitorum communis and M. extensor carpi radialis from the ectepicondyle. The superficial fibres, which are homologous to M. extensor carpi ulnaris, insert laterally on the ulnare (Miner, 1925; Walthall and Ashley-Ross, 2006). In anurans and salamanders, both muscles are fully differentiated; in these forms, M. extensor carpi ulnaris attaches to the ulnare only (Ribbing, 1907, 1938; Haines, 1939).

The muscle is relatively conservative in non-archosaurian reptiles. In all diapsids, it arises by a tendon from the distal part of the ectepicondyle. In some squamates, there is a second anchor on the proximal ulna, just distal to the olecranon process (Sanders, 1870, 1874). In all lepidosaurs, the tendon of insertion attaches to the pisiforme and the lateral side of the proximal base of metacarpal V (Mivart, 1870; Sanders, 1870, 1874; de Vis, 1884; Ribbing, 1907, 1938; Haines, 1939). In some forms, there is also a connection to the distal ulna (Miner, 1925; Abdala and Moro, 2006). M. extensor carpi ulnaris has the tendency to fuse with M. flexor carpi ulnaris (see section 'M. flexor carpi ulnaris' below) in some squamates, e.g., *Iguana* (Mivart, 1867; Rabl, 1916; Ribbing, 1938), forming a uniform muscle mass laterally on the forearm.

In chelonians, the muscle still forms a unified muscle with M. ectepicondylo-ulnaris, resembling the condition found in most urodeles. However, as in lepidosaurs, its tendon of insertion attaches to the pisiforme, ulnare, and metacarpal V laterally (Ribbing, 1907, 1938; Haines, 1939; Walker, 1973). There is no M. extensor carpi ulnaris in crocodilians (Ribbing, 1907; Haines, 1939).

Due to the reduction of the outer digits, birds have strongly modified the insertion of this muscle. It still arises by a tendon from the distal ectepicondyle. Distally, it runs through a furrow, the Incisura tendinosa, on the dorsal side of the distal condyle of the ulna, passes the dorsal side of the ulnare, and inserts on the intermetacarpal process on the proximocaudal side of metacarpal II (Gadow and Selenka, 1891; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Sullivan, 1962; Berger, 1966; McGowan, 1986; Vollmerhaus et al., 1992; Vanden Berge and Zweers, 1993). M. extensor carpi ulnaris is lost in *Apteryx* (McGowan, 1982). In *Struthio*, it is fused with M. ectepicondylo-ulnaris proximally and inserts on the base of metacarpal III (MacAlister, 1864; Gadow and Selenka, 1891).

DISCUSSION – M. extensor carpi ulnaris is present in all Reptilia with the exception of crocodilians. Therefore, it is probable that the muscle was still present at the base of the archosaurs, and disappeared on the crocodilian line only. Fusion to M. ectepicondylo-ulnaris seems to occur independently in several lineages; it is unclear whether the fused condition found in most urodeles (but not anurans) and turtles is plesiomorphic or secondarily acquired. In fossil archosaurs, a scar on the proximal dorsolateral corner of the ulnare and/or metacarpal V implies a plesiomorphic morphology of M. extensor carpi ulnaris, resembling lepidosaurs or turtles, because no other muscles insert at this location in extant tetrapods. However, given the loss of the muscle in crocodilians and its strongly modified insertion in birds, this reconstruction would only be a level III inference under strict appliance of the EPB.

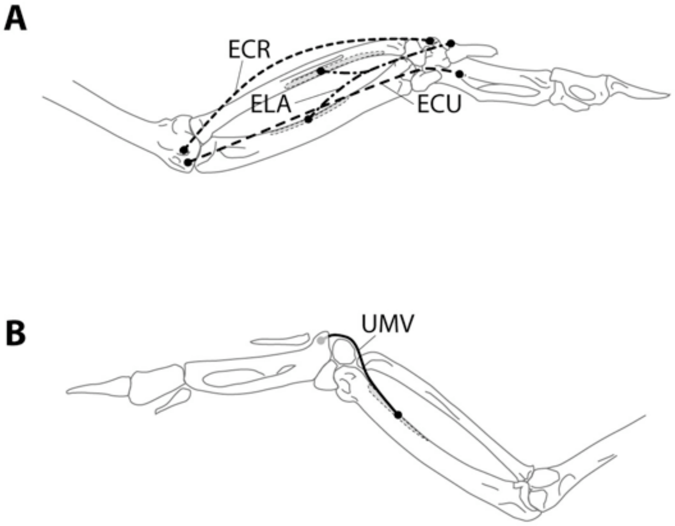

Figure 3-22. Probable avian homologues of M. pronator quadratus and of the carpal extensors of non-avian reptiles, as present in *Gallus* (A, dorsal view; B, ventral view). M. extensor longus alulae is probably a homologue of M. supinator manus; M. ulnometacarpalis ventralis is probably a homologue of M. pronator quadratus.

29. M. supinator manus (SM).

Synonyms:

M. extensor carpi (Haughton, 1866)

M. extensor ossis metacarpi pollicis (Mivart, 1867, 1870; Sanders, 1870, 1872, 1874; de Vis, 1884)

M. extensor pollicis longus (Gadow and Selenka, 1891; Fisher, 1946; Hudson and Lanzilloti, 1955, 1964; Berger, 1953, 1954, 1955, 1956a–c, 1957, 1960, 1966)

M. abductor metacarpi II (Ribbing, 1907)

M. abductor digiti I (Ribbing, 1907)

M. abductor pollicis longus (Rabl, 1916; Cong et al., 1998; literature on mammalian anatomy)

M. supinator brevis (Byerly, 1925)

M. extensor longus digiti II (Fisher and Goodman, 1955)

M. extensor indicis longus (Sullivan, 1962)

M. extensor longus alulae (McGowan, 1982, 1986; Schreiweis, 1982; Vanden Berge and Zweers, 1993)

M. extensor carpi radialis brevis (Meers, 2003; Fujioka, 1959)

M. abductor longus pollici (Abdala and Moro, 2006)

M. abductor et extensor digiti I (Walthall and Ashley-Ross, 2006)

Remarks: The extraordinarily long list of synonyms makes it difficult to identify a widely accepted term that may serve as a ‘common denominator’ for this muscle. The mammalian term listed in the NAV, ‘M. abductor pollicis longus’, has rarely been used in descriptions of reptilian anatomy. The term suggested by the NAA, ‘M. extensor longus alulae’, cannot be applied to non-avian diapsids, because these lack an alula. The only term that is not easy to confuse with names of other muscles is ‘M. supinator manus’, as applied by Miner (1925) and Haines (1939). Therefore, it is proposed here to use that term for this muscle.

DESCRIPTION – Originally, M. supinator manus (figs. 3-20, 3-21, 3-22) takes origin from the ulnar side of the antebrachium, crosses the wrist and inserts medially on the first metacarpal. In extant urodeles, the relatively short muscle arises from the dorsal side of the intermedium and the distal condyle of the ulna, sometimes also from the radius and centrale, and inserts medially on the proximal base of metacarpal I (Ribbing, 1907; Miner, 1925; Haines, 1939; Walthall and Ashley-Ross, 2006). Anurans have shifted the origin onto the central part of the fused antebrachial bones, while the insertion is situated at mid-length on the dorsal side of metacarpal I (Ribbing, 1938; Haines, 1939).

In lepidosaurs, M. supinator manus extends its origin proximally onto the craniomedial side of the distal ulnar shaft. Like in urodeles, the muscle attaches via a tendon to the base of metacarpal I medially (Mivart, 1867, 1870; Sanders, 1870, 1872, 1874; de Vis, 1884; Ribbing, 1907, 1938; Rabl, 1916; Byerly, 1925; Haines, 1939; Abdala and Moro, 2006). In some forms, there is also a connection to the ulnare (e.g., *Varanus*; Haines, 1939). Regarding *Sphenodon*, Miner (1925) mentioned that the muscle extends its origin medially onto the interosseal membrane between ulna and radius.

Most turtles exhibit a similar pattern of this muscle, but the area of origin may extend even further proximally in some forms, and covers almost the entire craniomedial side of the ulnar shaft. An origin from the intermedium is also preserved. As in lepidosaurs, the muscle inserts via a tendon on the base of metacarpal I (Ribbing, 1907, 1938; Haines, 1939; Walker, 1973). In some forms such as *Trionyx*, M. supinator manus extends medially and arises also from the lateral side of the radius.

A second, radial origin of M. supinator manus is a synapomorphic character of archosaurs. Moreover, the muscle extends its area of origin along the entire length of the shafts of both radius and ulna. The point of insertion has shifted onto the dorsoproximal edge of the radiale (Haughton, 1866; Ribbing, 1907, 1938; Haines, 1939; Meers, 2003). The homologous muscle of birds, M. extensor longus alulae, is topologically similar to the crocodilian muscle: There are two heads that arise from the ulna and the radius, fuse distally and insert together with M. extensor carpi radialis via a common tendon on the extensor process on the proximocranial (developmentally medial) side of the carpometacarpus, a region that is homologous to metacarpal I. Both heads may be differentially developed, depending on the taxon (Gadow and Selenka, 1891; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Sullivan, 1962; Berger, 1966; McGowan, 1982, 1986; Schreiweis, 1982; Vanden Berge and Zweers, 1993).

DISCUSSION – Phylogenetic inference implies that M. supinator manus was well developed in basal archosaurs, taking origin from both ulna and radius and extending relatively far proximally. Due to its fleshy type of origin, the exact extent is hard to delimit in fossil forms. Under consideration of non-archosaurian outgroups and the site of attachment in birds, it is most probable that the muscle in basal archosaurs inserted by a tendon medially on the base of metacarpal I, rendering the more proximal insertion in crocodilians a specialization that results from the modified proximal carpus.

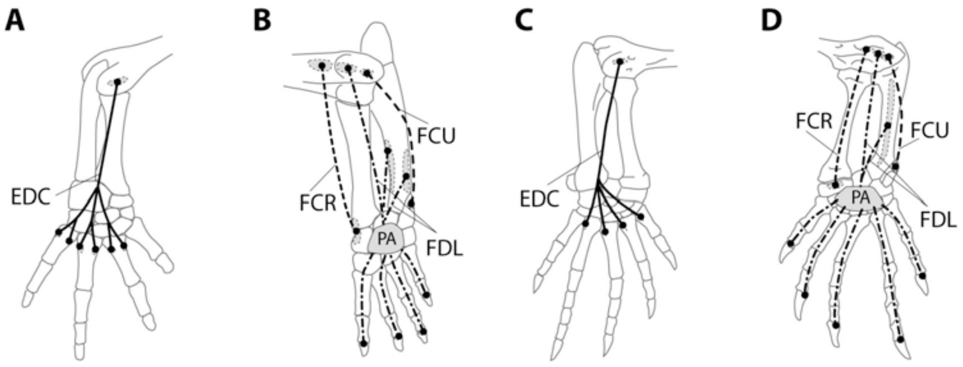

Figure 3-23. Superficial manual muscles of urodeles (A, dorsal view; B, ventral view) and *Sphenodon* (C, dorsal view; D, ventral view).

30. M. extensor digitorum communis (EDC).

Synonyms:

M. extensor carpi radialis (Mivart, 1867, 1870; de Vis, 1884)
M. extensor communis digitorum (Sanders, 1870; Byerly, 1925)
M. extensor longus digitorum (Sanders, 1872, 1874)
M. extensor digitorum communis longus (Rabl, 1916)
M. humerodorsalis (Haines, 1939)
M. extensor carpi ulnaris longus, ?M. extensor metacarpi I, ?M. extensor metacarpi IV (Meers, 2003)
M. extensor digitorum longus (Abdala and Moro, 2006)

Remarks: Most authors use the term 'M. extensor digitorum communis' or a similar perception for this muscle. This is also standardized in the NAA (Vanden Berge and Zweers, 1993). The alternative of Haines (1939), 'M. humerodorsalis', failed to gain wide acceptance in the literature. Meers (2003) misidentified this muscle as M. extensor carpi ulnaris, which is actually lost in crocodilians (Ribbing, 1907; see below, 'M. extensor carpi ulnaris'). Mm. extensores metacarpi I et IV *sensu* Meers (2003) are regarded here specialized parts of the primordial M. extensor digitorum communis, and are therefore treated in this section, too.

DESCRIPTION – M. extensor digitorum communis (figs. 3-23, 3-24, 3-25) is an evolutionary old muscle and is present in all tetrapods. In urodele amphibians, it arises by a tendon from the dorsal part of the ectepicondyle. Level with the wrist, it splits into four tendons that run to the distal phalanx on each finger. The Mm. extensores digitorum breves (see below) also control these tendons (Ribbing, 1907; Miner, 1925; Walthall and Ashley-Ross, 2006). In contrast, Haines (1939) described the amphibian M. extensor digitorum communis as attaching by split tendons proximally to both sides of each metacarpal. The grade of fusion of this muscle to the intrinsic extensors is probably subject to variation.

In amniotes, the origin remains on the dorsal ectepicondyle, but the connection between the long and short extensors is abandoned. In *Sphenodon*, the muscle distally splits into four tendons that insert laterally on the proximal bases of metacarpals I to IV, directly below the intermetacarpal joints (Miner, 1925; Ribbing, 1938; Haines, 1939). The tendon leading to metacarpal I is lost in squamates (Mivart, 1867; Sanders, 1870, 1872, 1874; de Vis, 1884; Ribbing, 1907, 1938; Rabl, 1916; Romer, 1922; Haines, 1939; Abdala and Moro, 2006). In addition, chameleons have lost the tendon that inserts on metacarpal II (Mivart, 1870; Ribbing, 1938).

Turtles kept the plesiomorphic split of each tendon into a medial and a lateral branch. These insert on both sides of the proximal base of all metacarpals, except of the medial side of metacarpal I, and the lateral side of metacarpal V (Ribbing, 1907, 1938; Haines, 1939; Walker, 1973). In contrast, the crocodilian M. extensor digitorum communis has lost its insertion on metacarpals I, IV, and V. Moreover, there is only a single tendon that inserts centrally on the bases of metacarpals II and III, the latter branch being very weakly developed and sometimes not observable (Ribbing, 1907, 1938; Haines, 1939; Meers, 2003). Meers (2003) described two additional extensors that arise from the proximal carpus, M. extensor metacarpi I medially and M. extensor metacarpi IV laterally. The former has its origin on the radiale and inserts proximally on metacarpal I, while the latter arises from the ulnare and attaches to metacarpal IV. There are no similar muscles in other vertebrates. Considering their points of insertion, it is possible that these muscles are specialized parts of a primordial M. extensor digitorum communis that lost connection to the main muscular body, and took a new attachment on the dorsal carpus; however, this assumption has to be tested by future research (see Conclusions below).

The avian M. extensor digitorum communis arises by a tendon from the ectepicondyle. Its tendon of insertion splits into two branches that run to the proximal phalanges of digiti I and II, respectively. The cranial (developmentally medial) branch inserts on the caudal side of the proximal phalanx of digit I, and the caudal branch attaches to the craniodorsal side of the proximal phalanx of digit II. The inserting tendon is correlated to a tubercle on the craniodorsal side of the distal ulna, where it is deflected towards the fingers just proximal to the split (Hudson and Lanzilloti, 1955, 1964; Sullivan, 1962; Schreiweis, 1982; Berger, 1966; McGowan, 1986; Vollmerhaus et al., 1992). In some forms, the medial branch has shifted its insertion proximally onto metacarpal I (Fisher and Goodman, 1955), or is completely reduced (Fisher, 1946; Vanden Berge and Zweers, 1993). The tendon leading to digit I misses in *Struthio* (Gadow and Selenka, 1891), and the entire muscle is lost in *Apteryx* (McGowan, 1982).

DISCUSSION – All reptilian lineages, with the exception of turtles, show a trend towards reduction of M. extensor digitorum communis, beginning with the connection to the outer digits. Phylogenetic inference implies that this muscle was present at the base of the archosaurs, but its grade of reduction at that point of evolution it is difficult to assess, even more so since the hands of *Euparkeria* are incompletely preserved (Ewer, 1965; see chapter 4). If the crocodilian Mm. extensores metacarpi I et IV are indeed derivates of M. extensor digitorum communis, it is probable that the latter muscle had tendons leading at least to metacarpals I to IV in basal archosaurs. The insertion of this muscle on the proximal phalanges in birds is here regarded as an autapomorphic specialization resulting from the coossification of the carpometacarpus.

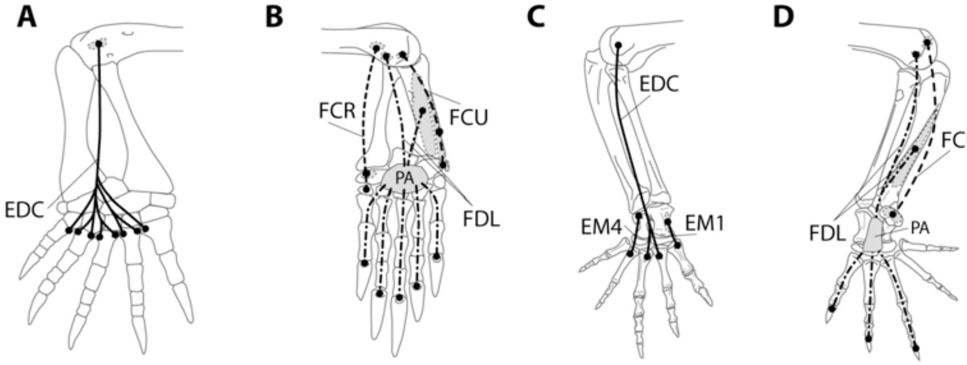

Figure 3-24. Superficial manual muscles of chelonians (A, dorsal view; B, ventral view) and *Alligator* (C, dorsal view; D, ventral view).

31. M. flexor carpi radialis (FCR).

There are no synonyms of this muscle known to the author.

DESCRIPTION – M. flexor carpi radialis (figs. 3-23, 3-24) is closely related to M. pronator teres. In urodele amphibians, both muscles still form a unified mass, M. flexor antebrachii et carpi radialis. The muscle arises by a tendon from the entepicondyle, and attaches distally to the medial side of the radius and the radiale (Ribbing, 1907, 1938; Walthall and Ashley-Ross, 2006). In squamates, M. flexor carpi radialis has lost its connection to M. pronator teres. The tendinous origin is situated ventrally on the entepicondyle, and the insertion is located medially on the radiale and distal carpus. In some forms, the insertion extends also onto metacarpal I, or the first phalanx of digit I (Mivart, 1867, 1870; Sanders, 1870, 1872, 1874; Ribbing, 1907, 1938; Rabl, 1916; Romer, 1922; Byerly, 1925; Miner, 1925; Haines, 1939; Abdala and Moro, 2006). The pattern is essentially the same in turtles (Ribbing, 1907, 1938; Walker, 1973).

M. flexor carpi radialis is completely lost in crocodilians and birds (Ribbing, 1907, 1938).

DISCUSSION – Phylogenetic inference implies that M. flexor carpi radialis was already lost in the last common ancestor of modern archosaurs. Since the muscle has no unambiguous osteological correlates in non-archosaurian reptiles, there is no positive evidence for the contrary. Therefore, it is assumed here that all archosaurs, including sauropodomorphs, lacked M. flexor carpi radials.

32. M. flexor carpi ulnaris (FCU).

There are no synonyms of this muscle known to the author.

DESCRIPTION – M. flexor carpi ulnaris (figs. 3-23, 3-24, 3-25) arises by a tendon from the distal part of the entepicondyle in most tetrapods. In urodele amphibians, its point of origin lies between that of M. flexor digitorum longus and M. entepicondylo-ulnaris, with which it may be intimately fused. The muscle inserts tendinously on the lateral side of the ulnare (Ribbing, 1907; Miner, 1925; Walthall and Ashley-Ross, 2006). Anurans have lost this muscle (Ribbing, 1907, 1938).

In all non-avian reptilians including crocodilians, the ventral side of the pisiforme serves as the main site of attachment for M. flexor carpi ulnaris (Haughton, 1866; Ribbing, 1907, 1938; Byerly, 1925; Miner, 1925; Haines, 1950; Cong et al., 1998; Meers, 2003). Some squamates developed a second origin from the proximal end of the ulna (Mivart, 1867, 1870; Sanders, 1872, 1874; de Vis, 1884; Rabl, 1916; Abdala and Moro, 2006). As mentioned above, the muscle may be fused to M. extensor carpi ulnaris in some species (e.g., *Iguana*: Mivart, 1867; Rabl, 1916), and to M. entepicondylo-ulnaris in others (Sanders, 1870). In turtles, the insertion may also extend to the lateral sites of the ulna, the ulnare, and metacarpal V. Fusion with M. entepicondylo-ulnaris is also observed in some cases (Ribbing, 1907, 1938; Walker, 1973).

Birds preserved the origin from the distoventral entepicondyle, where a slight groove or a short process, Processus flexorius, forms its osteological correlate. Distally, the tendon of insertion attaches to Processus muscularis of the ulnare (Gadow and Selenka, 1891; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Sullivan, 1962; Berger, 1966; Schreiweis, 1982; McGowan, 1986; Vollmerhaus et al., 1992; Vanden Berge and Zweers, 1993).

DISCUSSION – M. flexor carpi ulnaris is found in both groups of extant archosaurs and in non-archosaurian outgroups. Therefore, it can be concluded that the muscle was present at the base of the Archosauria. Furthermore, the uniform origin from the distal entepicondyle allows for the inference of a similar origin of this muscle in basal archosaurs. In these forms, the insertion of M. flexor carpi ulnaris probably was still located on the pisiforme: This element is the osteological correlate of M. flexor carpi ulnaris in all non-avian Reptilia, and the insertion on the ulnare in birds is here regarded as a reversal in connection with the modification of the avian hand skeleton.

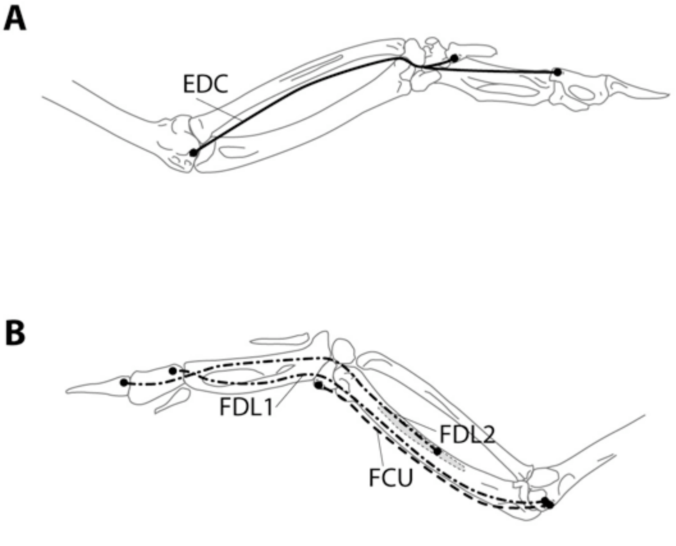

Figure 3-25. Superficial manual muscles of *Gallus* (A, dorsal view; B, ventral view).

33. M. flexor digitorum longus (FDL).

Synonyms:

M. palmaris, M. flexor digitorum communis (Haughton, 1866)
M. flexor profundus digitorum (Mivart 1867; Sanders, 1870, 1874)
M. flexor longus pollicis, M. flexor profundus digitorum (Mivart, 1870)
M. flexor perforans digitorum (Sanders, 1872)
M. flexor digitorum sublimis, M. flexor digitorum profundus (Gadow and Selenka, 1891; Rabl, 1916; Hudson and Lanzilloti, 1955, 1964)
M. flexor primordialis communis, Mm. flexores accessorii (Ribbing, 1907)
M. palmaris communis, M. palmaris profundus dorsalis (Miner, 1925)
M. flexor digitorum primordialis communis, M. flexor accessorius (Ribbing, 1938)
M. palmaris longus, M. flexor digitorum longus (Haines, 1950; Walker, 1973)

M. flexor digitorum communis, Mm. flexores accessorii (Walthall and Ashley-Ross, 2006)

M. flexor carpi ulnaris *partim*, M. flexor digitorum profundus (Fisher and Goodman, 1955)

M. flexor digitorum sublimis, M. flexor digitorum profundus (Hudson and Lanzilloti, 1955, 1964)

M. flexor digitorum superficialis, M. flexor digitorum profundus (other ornithological literature)

Remarks: This highly variable muscle complex has not always been treated as a single muscle. For example, Haines (1950) regarded the most superficial layer (his 'M. palmaris longus') as the remnant of an independent muscle that was present at the base of the amniotes, but was lost independently in most lineages with the exception of a few squamates. However, this concept never found general acceptance in the literature. Moreover, the remainder of M. flexor digitorum longus is so variable in number and morphology of its individual heads that any splitting into separate units would imply homologies that are hard to verify. Therefore, M. flexor digitorum longus is defined here as the entirety of all muscular heads arising from the distal humerus, forearm, and carpus, that contribute to the formation of the palmar aponeurosis. Due to the long list of synonyms, the nomenclature used here follows the most recent suggestions of Meers (2003) and Abdala and Moro (2006). The NAA concept cannot be applied in this case for two reasons: There are only two heads preserved in birds, and the terms used in ornithology, 'M. flexor digitorum profundus' and 'M. flexor digitorum superficialis', refer to intrinsic hand muscles in non-avian Reptilia (see below).

DESCRIPTION – The general pattern of M. flexor digitorum longus (figs. 3-23, 3-24, 3-25) is similar in all non-avian reptiles and urodele amphibians. One or more heads arise from the entepicondyle, and fuse distally to one or more heads that come from the ulna and the carpus. Together, all these individual muscular bodies contribute to a wide, tendinous palmar aponeurosis that spans over most of the palm. Plesiomorphically, the palmar aponeurosis gives rise to five tendons that attach ventrally on the base of the terminal phalanx of each finger.

In urodele amphibians, there is normally a single head coming from the entepicondyle, and two heads that arise fleshy from the distolateral and distomedial faces of the ulna ('Mm. flexores accessorii' of Ribbing, 1907). The origin of these heads may extend onto the ulnare and the lateral distal carpals (Ribbing, 1907, 1938; Miner, 1925; Walthall and Ashley-Ross, 2006).

For *Sphenodon*, Ribbing (1938) described only one ulnar head of M. flexor digitorum longus, but Byerly (1925) and Miner (1925) listed three: one head arises from the proximal ulna, just distal to the joint capsule; the second has a wide, fleshy origin from the ventral part of the ulna; and a third head attaches to the distolateral side of that bone. In addition, there is a single head arising form the entepicondyle, as in urodele amphibians (Ribbing, 1938; Byerly, 1925; Miner, 1925).

In contrast to *Sphenodon*, other lepidosaurs have developed up to four heads that arise from the entepicondyle. The most superficial layer ('M. palmaris longus' of Haines, 1950) has lost the connection to the palmar aponeurosis and inserts on the pisiforme, together with M. flexor carpi ulnaris, with which it tends to fuse (Sanders, 1872; Ribbing, 1907, 1938). Ribbing (1907) listed three heads arising from the ulna and ulnare, but other authors recognized only two (Mivart, 1867; Sanders, 1874; de Vis, 1884; Rabl, 1916; Haines, 1950) or one (Sanders, 1870, 1872; Abdala and Moro, 2006).

In turtles and archosaurs, the morphological pattern of M. flexor digitorum longus is more concise. Usually, there is one entepicondylar head that may be slightly subdivided, and one ulnar head that has its fleshy origin from the caudodistal part of the ulna (lateral to M. pronator quadratus) and ulnare (Haughton, 1866; Ribbing, 1907, 1938; Walker, 1973). Some species of turtles developed additional heads from the carpus (e.g., *Dermochelys*) or the radius (*Trionyx*) (Walker, 1973). In crocodilians, a superficial part of the entepicondylar head is fused to M. flexor carpi ulnaris (Ribbing, 1938), and the origin of the ulnar head extends onto the radiale and pisiforme. Meers (2003) regarded the most distal part of this muscle as an individual head, caput carpale. The palmar aponeurosis gives rise to only three tendons of insertion (but four in *Caiman*) that insert on the terminal phalanges of the inner fingers (Haughton, 1866; Ribbing, 1907, 1938; Cong et al., 1998; Meers, 2003).

Birds have reduced the palmar aponeurosis, which lead to individual tendinous insertions of the two parts of M. flexor digitorum longus. The entepicondylar head ('M. flexor digitorum superficialis') is very variable: in some forms, it has lost contact to the humerus, arising from the humerocarpal ligament only; in others, it is entirely tendinous or lost completely. Its tendon of insertion runs cranial to the Processus pisiformis of the carpus, which serves as a pulley, and inserts on the proximal phalanx of digit II. The ulnar head, 'M. flexor digitorum profundus', arises variably in position and extent from the ventral side of the ulna, its tendon of insertion running parallel to that of the entepicondylar head, and inserting on the terminal phalanx of digit II (Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Sullivan, 1962; McGowan, 1982, 1986; Schreiweis, 1982; Vollmerhaus et al., 1992; Vanden Berge and Zweers, 1993). In

Struthio, the tendon of insertion splits and runs to all digits, resembling the reptilian condition (MacAlister, 1864; Gadow and Selenka, 1891).

DISCUSSION – Sullivan (1962) observed that all heads of M. flexor digitorum longus develop in common with M. flexor carpi ulnaris from a single muscle primordium, explaining the frequent fusion of parts of this complex. The variable differentiation of the humeral part of M. flexor digitorum longus into several heads in squamates possibly reflects ecological specializations (e.g., arboreality). With respect to basal archosaurs, phylogenetic inference implies that these forms had an entepicondylar head that arose by a tendon from the humerus, and an ulnar head that arose fleshy from the caudal side of the ulna. Due to its fleshy nature, the exact extent of the origin of the latter is hard to delimit in fossil forms. Furthermore, it is not possible to reconstruct if these heads were subdivided, or if additional heads were present. Nevertheless, considering crocodilians and non-archosaurian reptiles, it is probable that basal archosaurs had a well-developed palmar aponeurosis and tendons of insertion running at least to digiti I-IV.

b) Intrinsic musculature of the hand

34. Mm. extensores digitorum superficiales (EDS).

Synonyms:

M. indicator (MacAlister, 1864)
M. extensor communis digitorum (Mivart, 1867)
M. extensor brevis digitorum (Sanders, 1870, 1872, 1874)
M. extensor communis (de Vis, 1884)
Mm. extensores breves digitorum superficiales (Ribbing, 1907)
M. extensor pollicis, Mm. extensores digitorum communis breves (Rabl, 1916)
M. extensor pollicis brevis, Mm. extensores communis digitorum breves (Byerly, 1925)
Mm. extensores digitorum communis breves (Miner, 1925)
Mm. extensores digitorum breves (Haines, 1939; Walker, 1973; Cong et al. 1998; Abdala and Moro, 2006)
M. extensor indicis longus, M. flexor metacarpi posterior (Fisher, 1946; Fisher and Goodman, 1955)
M. extensor indicis longus, M. ulnimetacarpalis dorsalis (Hudson and Lanzilloti, 1955, 1964)
M. extensor digiti terti longus, M. flexor et abductor digiti quarti (Fujioka, 1959)
M. extensor medius longus, M. ulnimetacarpalis dorsalis (Sullivan, 1962)
M. extensor indicus longus, M. ulnometacarpalis dorsalis (McGowan, 1982)
M. extensor longus digiti majoris pars proximalis, M. ulnometacarpalis dorsalis (Vanden Berge and Zweers, 1993, and other ornithological literature)

M. abductor et extensor digiti I (Walthall and Ashley-Ross, 2006)
includes M. extensor pollicis superficialis et indicis proprius (Meers, 2003)

Remarks: The set of short finger extensors has received various, albeit similar names. Following Meers (2003), the superficial and deep portions of these muscles are treated separately (see below, 'Mm. extensores digitorum profundi'). M. extensor pollicis, addressed as an independent muscle by several authors, is included in Mm. extensores digitorum superficiales throughout this work. Obviously, these muscles are strongly reduced and modified in birds. There is only one muscle that is easily recognizable as homologous to the superficial extensors of non-avian reptiles, M. extensor longus digiti majoris. Furthermore, Ribbing (1938) homologized the avian M. ulnometacarpalis dorsalis with this muscle complex, an opinion that is supported by embryological data (Sullivan, 1962) and therefore adapted here, too.

DESCRIPTION – Plesiomorphically, Mm. extensores digitorum superficiales (figs. 3-26, 3-27) are short muscles on the dorsal side of the hand that arise from the carpus and insert by a tendon dorsally on the terminal phalanx of each finger. In urodeles, the origins of all four extensors lie on the dorsal side of ulnare, intermedium, and centrale. The tendon of insertion fuses with that of M. extensor digitorum communis at the level of the metacarpal-phalangeal articulations (Ribbing, 1907, 1938; Miner, 1925; Haines, 1939; Walthall and Ashley-Ross, 2006). This connection to M. extensor digitorum communis is lost in amniotes (see above, 'M. extensor digitorum communis'). In *Sphenodon* and squamates, the Mm. extensores digitorum superficiales arise from similar positions as in urodele amphibians, but the most medial (I) or most lateral (V) muscle occasionally shifted its origin onto the distal ulna (Mivart, 1867; Sanders, 1870, 1872, 1874; de Vis, 1884; Ribbing, 1907, 1938; Rabl, 1916; Byerly, 1925; Miner, 1925; Haines, 1939; Abdala and Moro, 2006).

The picture is essentially the same in turtles. Usually, all extensors arise from the dorsal side of the ulnare and give rise to tendons of insertion that attach to the terminal phalanges of each finger (Ribbing, 1907, 1938; Walker, 1973). In some species, the origin of the medial parts shifted onto the distal end of the ulna (Haines, 1939). Due to the slender proximal carpus of crocodilians, Mm. extensores digitorum superficiales in this group arise also from the radiale (I-III), additional to the origins on the ulnare and distal ulna (IV-V). As in other non-avian reptiles, the tendons of insertion attach to the terminal phalanges (Ribbing, 1907, 1938; Haines, 1939; Meers, 2003). In addition, Meers (2003) described a thin, unusual muscle that arises between Mm. extensores digitorum superficiales I et II, and inserts by a split tendon on the proximal phalanges of digiti I and II. There is no indication if the presence of this ‘M. extensor pollicis superficialis et indicus proprius’ reflects individual or interspecific variation or is characteristic for all crocodilians, but according to its topology, the muscle is derived from the superficial extensors.

Birds have strongly modified this muscle complex. There is only one extensor that leads to the terminal phalanx of digit II, M. extensor longus digiti majoris. The muscle arises fleshy from the caudal side of the shaft of the radius, varying interspecifically in its extent and position. The second muscle that is probably derived from the Mm. extensores digitorum superficiales complex is M. ulnometacarpalis dorsalis. The tendinous origin of this muscle is in a rather plesiomorphic position, dorsally on the distal end of the ulna. Its fleshy insertion is located on the caudodorsal edge of metacarpal III in most birds (Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Sullivan, 1962; Berger, 1966; Schreiweis, 1982; McGowan, 1986; Vollmerhaus et al., 1992; Vanden Berge and Zweers, 1993). M. extensor longus digiti majoris is lost in *Apteryx* (McGowan, 1982), but well developed in *Struthio* (Gadow and Selenka, 1891).

DISCUSSION – The strong modification of this muscle complex in birds hampers its reconstruction in basal archosaurs by means of extant phylogenetic bracketing. Since the muscle is relatively conservative in non-avian reptiles, it is probable that it arose from the lateral carpus (ulnare and adjacent elements) in forms like *Euparkeria*. However, this is merely a Level II inference in terms of Witmer (1995).

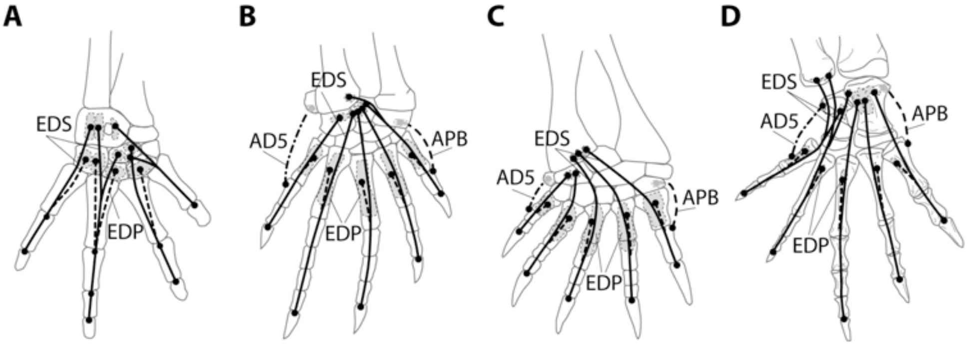

Figure 3-26. Dorsal views of intrinsic hand extensors and marginal abductors of urodeles (A), *Sphenodon* (B), chelonians (C), and *Alligator* (D). Shaded lines of action and attachment areas indicate muscles that lie on the remote side of the respective bone.

35. Mm. extensores digitorum profundi (EDP).

Synonyms:

Mm. interossei *partim* (Mivart, 1867)

Mm. extensores phalangorum (Mivart, 1870)

Mm. interossei dorsales (Sanders, 1870; Byerly, 1925; Walker, 1973)

M. extensor brevis digitorum *partim* (Sanders, 1872)

Mm. extensores breves digitorum profundes (Ribbing, 1907, 1938)

Mm. dorsometacarpales (Miner, 1925; Haines, 1939; Abdala and Moro, 2006)

M. flexor metacarpi brevis, M. extensor pollicis brevis (Fisher, 1946)

M. flexor metacarpi brevis, M. extensor brevis digiti II (Fisher and Goodman, 1955; Berger, 1966)

Distal head of M. extensor indicis longus, M. extensor pollicis brevis (Hudson and Lanzilloti, 1955, 1964)

M. extensor digiti terti brevis, M. extensor indicis (Fujioka, 1959)

M. extensor medius brevis, M. extensor indicis brevis (Sullivan, 1962)

M. extensor longus digiti majoris pars distalis, M. extensor brevis alulae (Vanden Berge and Zweers, 1993)

Mm. extensores digitorum breves (Walthall and Ashley-Ross, 2006)

Remarks: As for the superficial layer of the short finger extensors, the nomenclature used in the literature is inconsistent and often based on false homology assumptions. Therefore, the detailed and precise nomenclatorial concept of Meers (2003) is regarded as exemplary here. There are two potentially homologous muscles in birds: M. extensor brevis alulae and M. extensor longus digiti majoris pars distalis are topologically similar to Mm. extensores digitorum profundi of non-avian reptiles. Moreover, the second muscle has a close developmental relationship to the proximal (main) part of M. extensor longus digiti majoris (Sullivan, 1962).

DESCRIPTION – Mm. extensores digitorum profundi (figs. 3-26, 3-27) are closely related to Mm. extensores digitorum superficiales. The former set of muscles has its origins somewhat more distal than the latter, but both layers fuse and share common tendons of insertion that attach to the terminal phalanges of each digit (see above, ‘Mm. extensores digitorum superficiales’).

In Urodela, Mm. extensores digitorum profundi arise from the dorsal side of distal carpals 2, 3, and 4. The destinction between the superficial and the deep layer is not very clear in these forms (Ribbing, 1907, 1938; Haines, 1939; Walthall and Ashley-Ross, 2006). The sites of origin of these muscles have shifted distally in amniotes, onto the dorsal sides of each metacarpal. In *Sphenodon,* Miner (1925) found them to be divided into lateral and medial parts that insert on their respective sides of the metacarpal-phalangeal articulation. In turtles and crocodilians, Mm. extensores digitorum profundi exhibit fusion to the superficial layer. The destinction between both extensor layers is clearest in squamates. In this group, Mm. extensores digitorum profundi II-V also extended medially and attach to the proximolateral side of the preceding metacarpal (Ribbing, 1907, 1938; Haines, 1939; Walker, 1973; Meers, 2003; Abdala and Moro, 2006).

The avian muscle that is potentially homologous to M. extensor digiti profundi II is the distal head of M. extensor longus digiti majors. This part often misses, but is described for Galloanserae (Sullivan, 1962; Hudson and Lanzilloti, 1964; Vollmerhaus et al., 1992). It arises from the dorsal side of metacarpal II and fuses to the tendon of M. extensor longus digiti majors, which leads to the terminal phalanx of digit II (Vanden Berge and Zweers, 1993). Another muscle of birds, M. extensor brevis alulae, may represent M. extensor digiti profundi I: The origin is located craniodorsally on metacarpal I, and the tendinous insertion is situated on the base of the pollex (Gadow and Selenka, 1891; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Sullivan, 1962; Berger, 1966; McGowan, 1986). Both muscles are lost in *Apteryx*, but *Struthio* retained a M. extensor brevis alulae (Gadow and Selenka, 1891; McGowan, 1982).

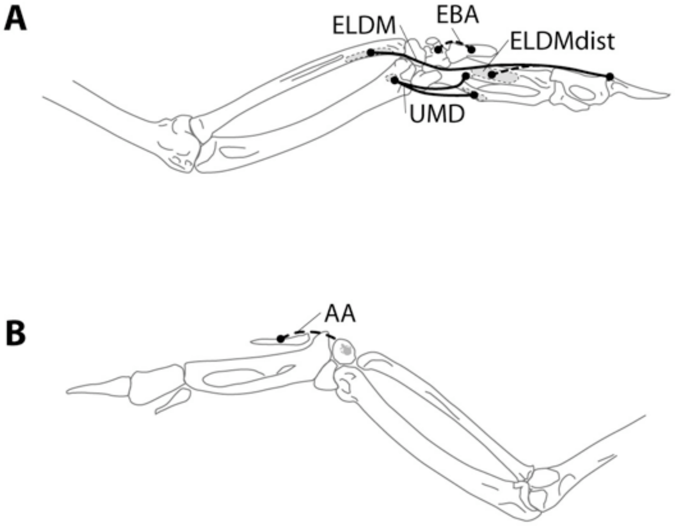

Figure 3-27. Probable avian homologues of the intrinsic hand extensors and marginal abductors of non-avian reptiles (*Gallus* in dorsal [A] and ventral [B] views). For explanations see text. Shaded lines of action and attachment areas indicate muscles that lie on the remote side of the respective bone.

DISCUSSION – As for Mm. extensores digitorum superficiales, the conservative morphology of Mm. extensores digitorum profundi observed in all non-avian reptiles strongly implies that the layer was present and arose from the dorsal sides of the metacarpals in basal archosaurs, too. This is also supported by avian anatomy:

If the muscles described above are indeed homologous to Mm. extensores digitorum profundi, their identical topology would allow for a level I inference of these muscles at least with respect to digiti I and II.

36. M. abductor pollicis brevis (APB).

Synonyms:

M. abductor pollicis (Fisher, 1946; Hudson and Lanzilloti, 1955, 1964)
M. abductor alae digiti II (Fisher and Goodman, 1955)
M. abductor indicis (Sullivan, 1962)
M. abductor alulae (McGowan, 1986; Vanden Berge and Zweers, 1993)
M. abductor metacarpi I (Meers, 2003)
M. abductor brevis pollici (Abdala and Moro, 2006)

Remarks: If mentioned at all, the majority of authors uses the name M. abductor pollicis brevis for this muscle. There are various alternatives in ornithological descriptions, but the standardization suggested by the NAA, 'M. abductor alulae', cannot be applied to non-avian reptiles for obvious reasons.

DESCRIPTION – M. abductor pollicis brevis (figs. 3-26, 3-27) probably is a medial derivate of M. extensor digiti superficialis I. The muscle is apomorphic for amniotes, although some species of amphibians developed a similar muscle (Ribbing, 1907). In lepidosaurs, it arises from the ventromedial part of the radiale and inserts by a tendon on the medioproximal corner of the first phalanx of digit I (Rabl, 1916; Miner, 1925; Haines, 1950). The site of insertion has shifted proximally onto metacarpal I in some forms (Sanders, 1870; Abdala and Moro, 2006).

In turtles, the origin of this muscle lies more distally, on the ventral face of distal carpal 1. The insertion is also proximomedially on the first phalanx of digit I (Walker, 1973). The homologous muscle in crocodilians arises fleshy from the ventromedial side of the radiale, and inserts by a tendon proximomedially on metacarpal I (Meers, 2003).

The avian M. abductor alulae consistently has a tendinous origin from the ventral side of the tendon of insertion of M. extensor carpi radialis, which is situated more or less level with the proximal base of metacarpal I. In some forms, there is also a second origin from the extensor process (Fisher and Goodman, 1955; McGowan, 1986; Vollmerhaus et al., 1992). The muscle inserts by a tendon cranioventrally on the proximal phalanx of digit I (Gadow and Selenka, 1891; Fisher, 1946; Hudson and Lanzilloti, 1955, 1964; Sullivan, 1962; Berger, 1966).

DISCUSSION – M. abductor pollicis is only seldomly observed in lepidosaurs, but its presence in *Sphenodon* and turtles suggests that it is a phylogenetically old muscle. Extant phylogenetic bracketing implies that the muscle was present at the base of the archosaurs, arising laterally from the ventral carpus and inserting onto the proximal phalanx of the first digit.

37. M. abductor digiti V (AD5).

Synonyms:

M. extensor metacarpi IX (Mivart, 1870)
M. abductor quinti digiti (Sanders, 1870, 1872)
M. opponens digiti minimi (Byerly, 1925)
M. abductor digiti minimi (Walker, 1973)
M. abductor metacarpi V (Meers, 2003)
M. abductor digitorum V (Abdala and Moro, 2006)

Remarks: The majority of authors who mention this muscle use the term 'M. abductor digiti V'. Therefore, this name is favored over Meers' (2003) recent alternative, which only reflects the crocodilian condition. Naturally, there is no homologous muscle in birds or lissamphibians, although a very similar muscle abducts digit IV in anurans.

DESCRIPTION – M. abductor digiti V (fig. 3-26) is very uniform in amniotes. Most authors interpreted this muscle as a specialized part of Mm. flexores digitorum profundi (e.g., Ribbing, 1907). In all non-avian reptiles, it arises from the pisiforme. The insertion is usually on the lateral side of the first phalanx of the fifth digit (Sanders, 1872; Ribbing, 1907; Rabl, 1916; Byerly, 1925; Haines, 1950; Walker, 1973). In some squamates and crocodilians, there is also a wide, fleshy insertion onto the lateral side of metacarpal V (Mivart, 1870; Sanders, 1870; Ribbing, 1907, 1938; Cong et al., 1998; Meers, 2003; Abdala and Moro, 2006).

DISCUSSION – Given the wide distribution and uniform topology of this muscle, it is highly probable that it was also present in basal archosaurs and only lost in theropod dinosaurs, due to the reduction of the outer fingers. However, under strict appliance of the EPB, this is merely a level II inference.

38. Mm. flexores digitorum superficiales (FDS).

Synonyms:

M. flexor sublimis digitorum (Mivart, 1867; Sanders, 1870; de Vis, 1884)
M. flexor brevis digitorum (Mivart, 1870)
M. flexor perforatus digitorum (Sanders, 1872, 1874)
Mm. flexores breves superficiales *partim* (Ribbing, 1907, 1938; Walthall and Ashley-Ross, 2006)
M. flexor palmaris (Rabl, 1916)

Mm. flexores communis digitorum (Byerly, 1925)
Mm. flexores breves sublimes *partim* (Miner, 1925)
M. flexor brevis sublimes (Haines, 1950)
M. flexor brevis superficialis (Walker, 1973)
M. flexor digitorum brevis superficialis (Meers, 2003)
Mm. flexores digiti brevis superficialis (Abdala and Moro, 2006)

Remarks: The most superficial set of flexor muscles in the palm has received various names. Most of them incorporate the adjective ‘brevis’, to emphasize the restriction of these muscles to the hand, and to contrast them with M. flexor digitorum longus. However, for simplification and standardization purposes, it is suggested here to use an abbreviated form, ‘Mm. flexores digitorum superficiales’. This also mirrors the terminology of the short extensors of the hand (see above, ‘Mm. extensores digitorum superficiales’). There are no homologous muscles in birds (Ribbing, 1938).

DESCRIPTION – The superficial flexors of the hand (fig. 3-28) are represented by a single, proximally undivided muscle mass in basal tetrapods, but show much specialization and differentiation in higher forms, especially in squamates. In amphibians, the muscle arises from the dorsal side of the palmar aponeurosis, splits into four slips that run to each digit, and inserts on the distal end of each metacarpal as well as ventrally on the bases of the proximal phalanges. Due to interspecific variation, the insertion may be displaced laterally, medially, or split to insert on both sides; this may also vary from digit to digit (Ribbing, 1907, 1938; Miner, 1925; Walthall and Ashley-Ross, 2006).

In contrast to anamniote tetrapods, Mm. flexores digitorum superficiales of amniotes arise from the ventral side of the palmar aponeurosis, directly under the skin of the palm. The Mm. lumbricales, which differentiated from the primordial Mm. flexores digitorum profundi (Ribbing, 1907), preserved the insertion on the dorsal side (see below, ‘Mm. lumbricales’). In *Sphenodon* and other lepidosaurs, the superficial layer is further subdivided into two distinct units. The superficial (ventral) unit arises from the transversal ligament, which spans between M. flexor carpi ulnaris and the pisiforme. One muscle head leads to each finger, splitting into a medial and a lateral slip that let the tendon of M. flexor digitorum longus pass between them. These slips reunite to insert in common on the flexor tubercle ventrally on the base of the penultimate phalanx of each digit. Dorsal to this layer, the deep division arises directly from the ventral side of the palmar aponeurosis. These muscles also split distally and attach to both sides of the metacarpal-phalangeal articulations of digiti II-IV (Byerly, 1925; Miner, 1925). The general picture is similar in squamates, but both layers are fused and have a common insertion (Mivart, 1867, 1870; Sanders, 1874; de Vis, 1884; Ribbing, 1907, 1938; Haines, 1950). Each tendon is often expanded distally and connects to other phalanges, in some forms also to the ungual (Abdala and Moro, 2006). Moreover, interspecific variation includes further subdivision of these muscles (often in certain digits only), reduction of the attachments to the proximal phalanges, and reduction of the deep layer in digit II or IV (Sanders, 1872; Ribbing, 1907, 1938; Rabl, 1916).

In chelonians and crocodilians, there is only one layer of Mm. flexores digitorum superficiales. As in other amniotes, this set of muscles arises from the ventral side of the palmar aponeurosis in chelonians. One muscle head leads to each digit, splits distally and inserts on both sides of the ventral base of the proximal phalanx (Ribbing, 1907, 1938; Walker, 1973). The situation is similar in crocodilians, but in many forms there is no strong palmar aponeurosis, making the superficial flexors to arise also from the distal carpals. The exact pattern of insertion varies from digit to digit, interspecifically, and individually (Ribbing, 1907, 1938; Cong et al., 1998; Meers, 2003).

There are no homologous muscles in birds (Ribbing, 1938). The palmar aponeurosis is lost, and flexion of the phalanges is controlled by M. flexor digitorum longus only.

DISCUSSION – A subdivision of Mm. flexores digitorum superficiales into a superficial and a deep layer seems to be a specialization restricted to lepidosaurs. Based on chelonian and crocodilian anatomy, basal archosaurs can be reconstructed with a single-layered set of Mm. flexores digitorum superficiales that arise from the palm, potentially from a palmar aponeurosis, and insert primarily on both sides of the flexor tubercles of the non-ungual phalanges. As for many hand muscles, the strong modification of the avian manus in this case hampers the appliance of the Extant Phylogenetic Bracket: strict phylogenetic inference by consideration of just the two extant archosaur groups renders the presence of these muscles in dinosaurs only equivocal.

39. M. flexor pollicis brevis (FPB).

Synonyms:

Mm. contrahentes digitorum *partim* (Ribbing, 1907; Miner, 1925)
M. adductor pollicis (Rabl, 1916)
M. flexor pollicis (Byerly, 1925)
?M. flexor pollicis (Fisher, 1946; Hudson and Lanzilloti, 1955, 1964)
?M. flexor digiti II (Fisher and Goodman, 1955)

?M. flexor indicis (Sullivan, 1962)

?M. flexor alulae (Schreiweis, 1982; McGowan, 1986; Vanden Berge and Zweers, 1993)

M. flexor digitorum V transversus I (Abdala and Moro, 2006)

Remarks: This muscle has only rarely been reported. Accordingly, homologies are difficult to assess, and it is possible that such a muscle developed from Mm. flexores digitorum superficiales independently in several lineages. Ribbing (1907) and Miner (1925) described this muscle, but interpreted it as a relict of the amphibian Mm. contrahentes. The name used by Haines (1950) in his general account on the hand flexors seems to be the most established one, and is therefore applied here, too. The NAA term 'M. flexor alulae' cannot be applied to non-avian reptiles, and it is also far from clear if that muscle is homologous to M. flexor pollicis brevis of some non-avian reptiles. Therefore, M. flexor alulae is only tentatively assigned to M. flexor pollicis brevis in this review (see Discussion below).

DESCRIPTION – A M. flexor pollicis brevis (fig. 3-28) has only been described in few genera of lepidosaurs: *Sphenodon* (Byerly, 1925; Miner, 1925), *Chamaeleo* (Mivart, 1870), *Iguana* (Rabl, 1916), and *Varanus* (Haines, 1950). 'M. flexor digitorum V transversus I' of *Liolaemus* (Abdala and Moro, 2006) seems to be topologically similar, but was not figured by the authors. In these forms, the muscle arises from the distal carpals (in *Varanus* more proximolaterally from the ulnare), runs obliquely across the palm, and inserts on the proximal base of the first phalanx of digit I.

M. flexor alulae of birds is similar insofar as it usually arises close to the pisiform process from the proximal carpometacarpus (fig. 3-29). Therefore, it crosses the carpus, and inserts caudoventrally on the proximal base of the pollex in many forms (Fisher, 1946; Fisher and Goodman, 1955; Sullivan, 1962; Hudson and Lanzilloti, 1964; Vollmerhaus et al., 1992).

DISCUSSION – M. flexor alulae is treated in this section because of its topological similarity to M. flexor pollicis brevis, but there is no strong evidence for the homology of both muscles. The avian muscle might also represent a specialized part of Mm. lumbricales or Mm. flexores digitorum profundi. The absence of M. flexor pollicis brevis in crocodilians and turtles does not support an equalization of both muscles. However, the systematic position of turtles is still under dispute, and crocodilians may secondarily have lost the muscle. Since this issue cannot be resolved under the scope of this work, it is tentatively assumed here that basal archosaurs and sauropodomorphs lacked a M. flexor pollicis brevis.

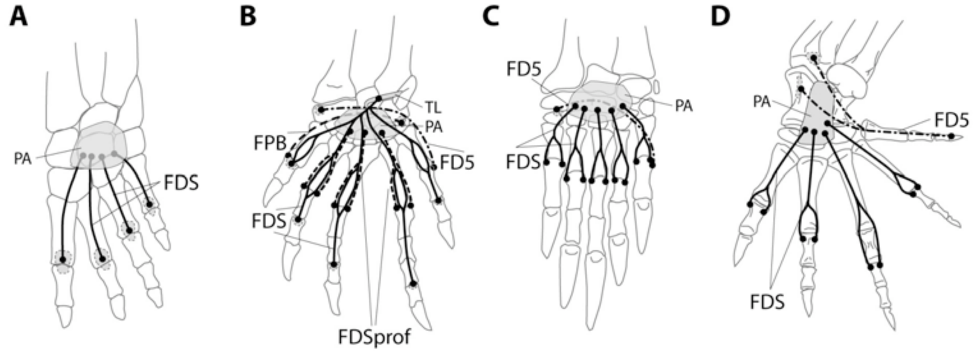

Figure 3-28. Ventral views of the superficial hand flexors of urodeles (A), *Sphenodon* (B), chelonians (C), and *Alligator* (D). Shaded lines of action and attachment areas indicate muscles that lie on the remote (dorsal) side of the palmar aponeurosis.

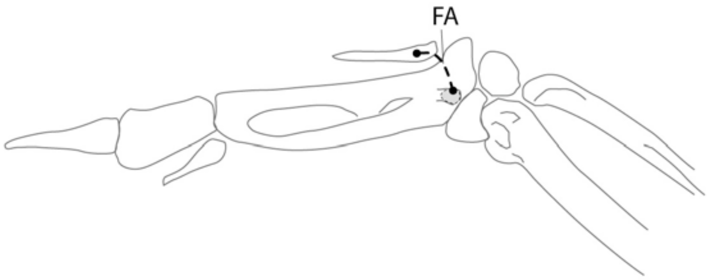

Figure 3-29. M. flexor alulae of *Gallus* (ventral view), a possible homologue of M. flexor pollicis brevis. Abbreviations not listed elsewhere: FA, M. flexor alulae.

40. M. flexor digiti V (FD5).

Synonyms:

M. flexor brevis minimi digiti (Mivart, 1870)
M. adductor quinti digiti (Sanders, 1872)
M. adductor minimi digiti (de Vis, 1884)
Mm. contrahentes digitorum *partim* (Ribbing, 1907; Miner, 1925)
?M. adductor digiti V (Rabl, 1916)
M. abductor digiti minimi (Byerly, 1925)
M. flexor brevis digiti V (Haines, 1950)
M. adductor digiti minimi (Walker, 1973)
M. flexor digiti quinti brevis, M. opponens digiti quinti (Cong et al., 1998)
M. flexor digiti V, M. transversus palmaris (Meers, 2003)
M. flexor digitorum V transversus II (Abdala and Moro, 2006)

Remarks: This muscle has been reported frequently in several non-avian reptiles. Regarding its terminology, the name recently used by Meers (2003) has been selected. It is assumed here that 'M. transversus palmaris' of Meers (2003) is a specialized part of this muscle. Therefore, 'M. transversus palmaris' also is treated in this section. Naturally, there is no homologous muscle in birds.

DESCRIPTION – A specialized M. flexor digiti V that crosses the palm from medial to lateral is present in many lepidosaurs, including *Sphenodon* (fig. 3-28). Its origin is always located in the carpus, often on the distal carpals (Sanders, 1872; Byerly, 1925; Miner, 1925; Walker, 1973), but it may also have shifted onto the radiale (Haines, 1950; Abdala and Moro, 2006), metacarpal I (de Vis, 1884), the palmar aponeurosis (Mivart, 1870; Ribbing, 1907; Rabl, 1916), or the ulnare (Miner, 1925). The muscle inserts medially on the base of the first and in some forms also on the second phalanx of digit V. Like M. flexor pollicis brevis, it runs deep to the palmar aponeurosis in many forms, including turtles, but ventral (superficial) to Mm. flexores digitorum superficiales in crocodilians. At first glance, this pattern speaks against a homology of both muscles. However, if regarded as a derivate of the lateral rim of the superficial flexor mass (Ribbing, 1907), it can be imagined how such a muscle might shift its origin relative to the flexor tendons during ontogeny. Therefore, the different relative position of M. flexor digiti V in these groups does not necessarily obviate homology.

In crocodilians, M. flexor digiti V has differentiated into two parts, the larger one of those called 'M. transversus palmaris' by Meers (2003) and 'M. opponens digiti quinti' by Cong et al. (1998). This muscle complex arises from the radiale, in some forms also from the caudomedial end of the radius, and inserts ventromedially on metacarpal V and all phalanges of digit V (Ribbing, 1907; Cong et al., 1998; Meers, 2003).

DISCUSSION – It is evident that M. flexor digiti V is a specialized part of Mm. flexores digitorum superficiales (Ribbing, 1907). However, the different patterns of this muscle in crocodilians, turtles, and lepidosaurus raises doubts about its strict homology in these groups. This question should be examined by additional anatomical and embryological studies in the future, but is beyond the scope of this work. Since M. flexor digiti V is absent in birds and does not leave any unambiguous osteological correlates, an assessment of its presence in basal archosaurs can only be speculative.

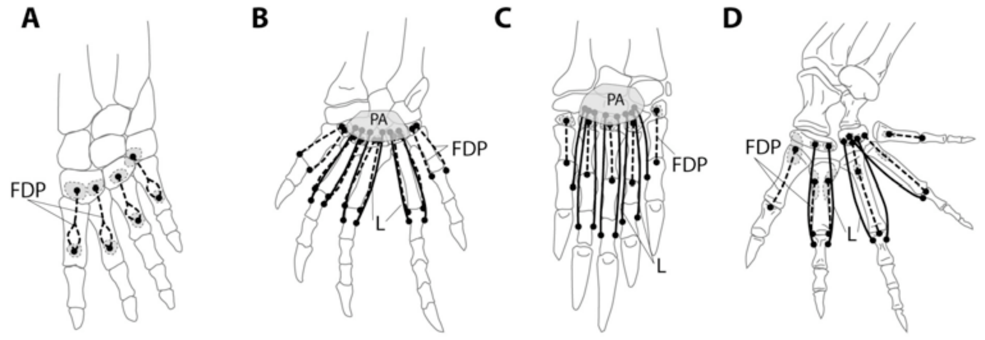

Figure 3-30. Deep intrinsic manual flexors of urodeles (A), *Sphenodon* (B), chelonians (C), and *Alligator* (D). Shaded lines of action and attachment areas indicate muscles that lie on the remote (dorsal) side of the palmar aponeurosis.

41. Mm. lumbricales (L).

Synonyms:

M. flexor perforatus digitorum *partim* (Sanders, 1872)
Mm. interossei *partim* (de Vis, 1884)
Mm. flexores breves sublimes *partim* (Miner, 1925)
Mm. lumbricales, Mm. contrahentes (Haines, 1950)
Mm. lumbricalis (Abdala and Moro, 2006)

Remarks: The second layer of hand flexors was correctly identified as 'Mm. lumbricales' by most authors. Exemptions are listed above.

DESCRIPTION – As mentioned earlier (see 'M. flexores digitorum superficiales' above), Mm. lumbricales (fig. 3-30) are restricted to amniotes. They are characterized by their origin from the dorsal side of the palmar aponeurosis. In *Sphenodon*, a set of six muscles arises distally from the palmar aponeurosis and attaches in pairs to both sides of the proximal phalanges of digiti II to IV (Byerly, 1925; Miner, 1925; Ribbing, 1938). In squamates, Mm. lumbricales have differentiated into a superficial and a deep portion, the latter arising more proximally. The number of these muscles and their sites of insertion on the digits are interspecifically highly variable (Mivart, 1867, 1870; Sanders, 1870, 1872; de Vis, 1884; Ribbing, 1907; Rabl, 1916; Haines, 1950; Abdala and Moro, 2006).

Some genera of chelonians (e.g., *Pseudemys*) more clearly illustrate the plesiomorphic pattern of Mm. lumbricales. In these forms, the set of muscles is symmetrical: Eight heads arise from the dorsal side of the palmar aponeurosis and run along the sides of the digits to insert on both sides of the penultimate phalanx of digiti II to IV, laterally on digit I, and medially on digit V. However, other turtles have reduced the number of Mm. lumbricales and modified the pattern of insertion (Ribbing, 1907, 1938; Walker, 1973).

In crocodilians, the number of Mm. lumbricales is reduced, too. They insert in pairs on the bases of the proximal phalanges of digiti II and III, and a fifth M. lumbricalis attaches to the medial side of the proximal phalanx of digit IV (Ribbing, 1907, 1938; Cong et al., 1998; Meers, 2003). No homologues of these muscles exist in birds (Ribbing, 1938).

DISCUSSION – The presence of Mm. lumbricales is a plesiomorphic feature of all amniotes, and some of them are also preserved in crocodilians. Therefore, it can be concluded that basal archosaurs possessed a number of these muscles. However, the number and sites of insertion of these muscles are so variable in all groups of non-avian reptiles that it seems impossible to reconstruct the pattern in extinct forms on the basis of present knowledge.

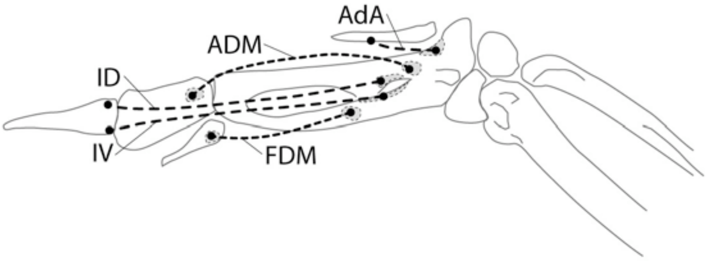

Figure 3-31. Probable avian homologues of Mm. flexores digitorum profundes and Mm. interossei of non-avian reptiles (*Gallus* in ventral view).

42. Mm. flexores digitorum profundi (FDP).

Synonyms:

Mm. interossei palmares (Sanders, 1872)
Mm. interossei pars m. flexor brevis (de Vis, 1884)
Mm. flexores breves profundi (Ribbing, 1907; Miner, 1925; Haines, 1950)
Mm. interossei (Rabl, 1916)
M. abductor major digiti III, M. flexor digiti IV (Fisher and Goodman, 1955)
M. abductor medius, M. flexor digiti quarti (Sullivan, 1962)
M. abductor indicis, M. flexor digiti III (Fisher, 1946; Hudson and Lanzilloti, 1955, 1964)
Mm. interossei volares (Walker, 1973)
M. abductor digiti majoris, M. flexor digiti minoris (Vanden Berge and Zweers, 1993)
Mm. interossei manus (Cong et al., 1998)
Mm. flexores digiti brevis profundus (Abdala and Moro, 2006)

Remarks: The deep flexors of the hand are poorly understood. More detailed studies on reptilian hand anatomy are necessary to fully understand their various patterns in the future. This becomes evident by the inconsistent terminology, as many authors often regarded Mm. flexores digitorum profundi as Mm. interossei (see synonymy list above). The corresponding muscles of birds are probably M. abductor digiti majoris and M. flexor digiti minimi, because these muscles are topologically similar to Mm. flexores digitorum profundi of non-avian reptiles. However, this hypothesis should also be further tested by future examinations.

DESCRIPTION – The deepest flexor layer of the palm (fig. 3-30) arises from the distal carpals and inserts onto the metacarpal of each finger in modern amphibians. Close to the insertion, each belly bifurcates to give way for the origin of M. flexor minimus, an accessory flexor not found in amniotes (Ribbing, 1907, 1938; Miner, 1925; Abdala and Moro, 2006).

In lepidosaurs, Mm. flexores digitorum profundi take origin from the distal carpals, bifurcate in some forms, and attach to both sides of the proximal phalanx of each digit. This plesiomorphic pattern may be modified by the loss of one ore more bellies, normally those of the outer fingers (Mivart, 1867; Sanders, 1872; de Vis, 1884; Ribbing, 1907, 1938; Rabl, 1916; Haines, 1950; Abdala and Moro, 2006).

Chelonians show the same plesiomorphic pattern as lepidosaurs, but the muscle complex has not been studied in detail in many species of turtles (Walker, 1973). Crocodilians have shifted the origin of these muscles onto the metacarpals, but there may still be a connection to the distal carpals. Some heads (e.g., that of the second digit in *Alligator mississippiensis*) show a clear differentiation into a lateral and a medial part. As in other Reptilia, all heads insert on the bases of the proximal phalanges of their respective digit (Ribbing, 1907, 1938; Cong et al., 1998; Meers, 2003).

The two avian muscles that are probably homologous to Mm. flexores digitorum profundi, M. abductor digiti majoris and M. flexor digiti minoris, arise from the ventral aspects of their respective metacarpals, the former more cranially on the bone, the latter more caudally (fig. 3-31). Both muscles insert on the base of the proximal phalanx of their respective digit, M. flexor digiti minoris being associated with a distinct tubercle on the caudal side of the bone (Gadow and Selenka, 1891; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Sullivan, 1962; Berger, 1966; Schreiweis, 1982; McGowan, 1986; Vollmerhaus et al., 1992).

DISCUSSION – Mm. flexores digitorum profundes are plesiomorphic muscles that must have been present at the base of the archosaurs. Phylogenetic inference, under acceptance of the homologues proposed above, implies that these forms already had transferred the origin of this muscle complex distally onto the metacarpals. The insertions of these muscles are constantly located on the proximal phalanges in all amniotes, rendering a similar course in basal archosaurs most probable.

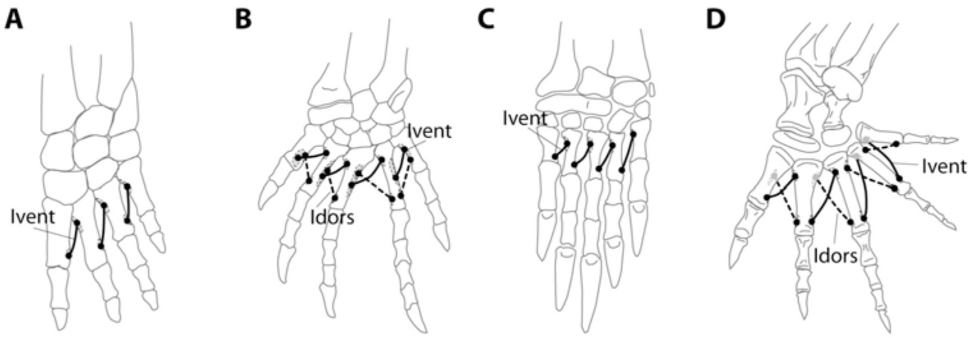

Figure 3-32. Mm. interossei in urodeles (A), *Sphenodon* (B), chelonians (C), and *Alligator* (D). Shaded attachment areas and lines of action indicate muscles that lie on the remote side of the respective bone.

43. Mm. interossei (I).

Synonyms:

Mm. flexores breves profundi (Miner, 1925)
Mm. interdigitales *partim* (Ribbing, 1938)
Mm. interossei, Lig. intermetacarpales (Haines, 1950)
M. adductor alulae (Vanden Berge and Zweers, 1993)

Remarks: Aside from the confusion regarding the proper identification of Mm. interossei mentioned above (section ‘Mm. flexores digitorum profundi’), the plesiomorphic morphology of this layer is not entirely understood. Moreover, parts of this muscle complex are reduced or lost in almost all reptiles, and not much is known about its morphology in turtles. Therefore, the plesiomorphic pattern of organization described here is a hypothesis that was extracted from published descriptions, but again should be tested by future examinations.

DESCRIPTION – Mm. interossei (fig. 3-32) plesiomorphically consist of two distinct layers of muscles that interconnect the metacarpal bones. The muscles of the dorsal layer have their origin laterally on the proximal bases of metacarpals I to IV and run distolaterally to attach to the distal end of the laterally adjacent metacarpal in each case. The ventral layer runs vice versa: There are four muscles originating on the proximomedial bases of metacarpals II to V, each running distomedially and inserting distally on the lateral side of the preceding metacarpal.

By now, this pattern has not been recognized in any living tetrapod. In amphibians and chelonians, only the ventral layer has been described (Miner, 1925; Ribbing, 1907, 1938; Walthall and Ashley-Ross, 2006). Lepidosaurs show both layers, but the dorsal part is reduced to faint tendinous bands, the intermetacarpal ligaments (Ribbing, 1907; Haines, 1950).

Crocodilians have both layers fully developed, but some heads of the dorsal layer have modified their origin and lie ventral to their counterpart of the plesiomorphically ventral layer, leading to confusion in nomenclature of these muscles (Meers, 2003:fig. 18; fig. 3-32). Ribbing (1907, 1938) could not find the two lateral Mm. interossei dorsales (between metacarpals III-IV and IV-V) in his sample of crocodilians.

There are no clear homologues of these muscles in birds. The muscles described as 'M. interosseus dorsalis' and 'M. interosseus ventralis' (fig. 3-31) both arise fleshy from the borders of the interosseous space, i.e. the caudal side of metacarpal II and the cranial side of metacarpal III. The dorsal part attaches cranially on the second phalanx of digit II, and the ventral part caudally on the same phalanx. Embryological data indicate that these muscles are composed of several fused primordial hand muscles (Dylevsky, 1968). Another possible homologue to Mm. interossei, M. adductor alulae (fig. 3-31), arises fleshy from the cranial side of metacarpal II and inserts on the caudal face of digit I (MacAlister, 1864; Gadow and Selenka, 1891; Fisher, 1946; Fisher and Goodman, 1955; Hudson and Lanzilloti, 1955, 1964; Sullivan, 1962; Berger, 1966; Schreiweis, 1982; McGowan, 1986; Vollmerhaus et al., 1992).

DISCUSSION – Since it cannot be convincingly shown that the avian muscles described here are homologues of Mm. interossei of non-avian reptiles, appliance of the Extant Phylogenetic Bracket is difficult in this case. Nevertheless, considering their presence in all other tetrapods, it is probable that these muscles existed in basal archosaurs and early dinosaurs, too. However, their exact configuration is hard to reconstruct, because there are no unambiguous osteological correlates. Moreover, it is unclear whether the crocodilian condition is indeed closest to the hypothetical plesiomorphic condition described above, or secondarily acquired, leaving the question about the morphology of basal dinosaurian Mm. interossei open to speculation.

Conclusions

As already mentioned at the beginning of this chapter, it became evident throughout this review how sensitive EPB reconstructions are to the choice of extant sample taxa. For example, Nicholls and Russell (1985) used *Chamaeleo* as a model for lepidosaurs; Jasinoski et al. (2006) chose *Caiman* to represent crocodilians. However, it has been demonstrated that both genera are highly derived with respect to several forelimb muscles, and are therefore not suited *per se* as representatives of an entire clade.

Moreover, the limits of the EPB methodology in general became apparent. The method works well if applied to closely related forms (for example, reconstructing the myology of *Ursus spelaeus* by studying modern Ursidae: Bryant and Seymour, 1990), but problems arise if both extant sample taxa follow totally different *bauplans*, due to long, independent evolutionary histories of both groups. In case of birds and crocodilians, both lines diverged at least 240 million years ago, leaving enough time for numerous evolutionary novelties on both branches. Crocodilians are no archetypic forms that may serve as a 'starting point' for dinosaur forelimb evolution, but instead are strongly modified, especially with respect to the pectoral girdle and wrist. These osteological novelties definitely reflect myological innovations, too. The challenge is to identify these novelties, and to sort them out from symplesiomorphic characters, in one word, to polarize the root of the EPB, an important step left out by recent studies (e.g., Jasinoski et al., 2006). The only way to polarize is by outgroup comparision, but the available outgroups (lepidosaurs, mammals, lissamphibians) are only tips of even longer branches, which are likely to have acquired their own evolutionary novelties, too. Since the fossil record in most cases cannot provide additional information on soft tissue evolution, it is virtually impossible by means of comparative anatomy alone to identify homoplastic characters, which are also likely to exist in the muscle anatomy of these groups. Hopefully, future progression in genetics and developmental biology will help to understand the evolutionary history of the tetrapod muscular apparatus better, which may open the door to more reliable reconstructions of extinct forms.

4 Forelimb anatomy of basal archosaurs and ornithodirans: Facts and Fictions

Introduction

The evolutionary history of the Dinosauria began in the Middle Triassic, when the two clades emerged that form the crown group Archosauria, Crurotarsi and Ornithodira. First representatives of both groups of archosaurs are found in the Ladinian of South America, and by the Late Carnian, all major groups of dinosaurs had left first traces in the fossil record (see Benton, 2004). However, comparatively little is still known about the root of the dinosaurs, since only few taxa have been identified that fill the evolutionary gap between the relatively conservative *bauplan* of basal archosauromorphs and the advanced locomotory system of early bipedal dinosaurs, such as *Herrerasaurus* or *Coelophysis*. Although Sereno's (1991, 1997) hypothesis (that the success of the first dinosaurs is strongly correlated with the development of fully upright hindlimbs for swift, obligate bipedal locomotion) is widely accepted, the dinosauromorph material on which this idea is based is incomplete and partially found in multi-taxon assemblages. Therefore, the quality of the data that led to this interpretation has to be critically tested. Moreover, most studies concentrated on hindlimb anatomy only (e.g., Sereno, 1991, 1997; Novas, 1996; Carrano, 2000; Hutchinson, 2006), without considering other important factors such as relative trunk length and transformations of the forelimb anatomy. By examination of the anatomy and function of the forelimb of early archosaurs and ornithodirans, this chapter determines what we actually can know about the beginning of dinosaurian forelimb evolution. A critical re-examination raises some doubts about current perceptions on the locomotory behavior and ecology of these small archosaurs, which gave rise to a group that should dominate the terrestrial faunas of the planet for the following 155 million years.

Data quality

The relationships of the various groups at the base of the archosaurs are not entirely clear (e.g., the phylogenetic position of Proterochampsidae; Benton, 2004). However, *Euparkeria capensis* from the Anisian of South Africa is closely related to the crown group Archosauria (see Benton, 2004, for a review) and may serve as a 'prototype' for the last common ancestor of dinosaurs and crocodilians. Although this form lacks several archosaurian autapomorphies (e.g., *Euparkeria* retains palatinal teeth, and misses numerous ankle characters; Sereno, 1991; Juul, 1994; Parrish, 1997; Gower and Weber, 1998; Benton, 2004), the anatomy of its forelimbs makes a good starting point for tracking the evolution of this organ complex in dinosaurs.

The taxon *Euparkeria* was erected by Broom (1913a), and its anatomy and relationships were shortly described in a successive paper by the same author (Broom, 1913b). Later, Ewer (1965) published the most detailed study to date on the anatomy of this form. The holotype, SAM 5867, is a largely articulated skeleton that is embedded in a block of sandstone. The specimen preserves the complete shoulder girdle, the interclavicle, clavicles, and the right forelimb without the manus. However, due to the type of preparation, these elements cannot be examined from all sides. There are several referred elements that were fully freed from matrix and provide additional information, including two left scapulae, a left coracoid, three left humeri, and two left radii (SAM 6047, 6048, 7696, 7700). Moreover, Ewer (1965) described and figured an incomplete metacarpus (SAM 13666, 13667), which unfortunately could not be examined personally during this study. According to Ewer (1965), all specimens come from the same locality and were probably found together in a death assemblage.

The basal ornithodiran *Scleromochlus taylori* from the Late Carnian Lossiemouth Sandstone Formation of the Elgin area, Scotland, was first described by Woodward (1907). Its anatomy was examined in detail only recently (Benton, 1999). Remains of several small skeletons are preserved as natural molds in a coarse-grained sandstone, rendering a detailed study of minute structures and bone surfaces impossible. Only in two specimens, BMNH R3556 and BMNH R3914, are traces of the forelimbs visible, but no clavicles or hands could be identified. In recent phylogenetic analyses, *Scleromochlus* plots as sister group to Pterosauria+Dinosauria (Benton, 1999, 2004), and is therefore the basal-most ornithodiran currently known.

The Ladinian sediments of the Los Chañares Formation of Argentina produced several early ornithodirans that stand closer to dinosaurs than to pterosaurs (Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991; Novas, 1992, 1996; Juul, 1994; Bennett, 1996; Benton, 1999, 2004). These include *Lagerpeton, Lagosuchus, Marasuchus, Lewisuchus*, and *Pseudolagosuchus*, which may be a subjective junior synonym of the former (Arcucci, 1997). Only *Lagosuchus, Marasuchus,* and *Lewisuchus*, which are more closely related to dinosaurs than *Lagerpeton* (Novas, 1992, 1996; Juul, 1994; Sereno, 1997; Benton, 1999, 2004), comprise remains of the forelimb. All specimens were found on slabs of volcanogenic concretions (Rogers et al., 2001), often together with remains of other taxa of archosaurs.

The holotype of *Lagosuchus talampayensis* (PVLR 09) is a fragmentary skeleton that was found in close association with the holotypic skeleton of the sphenosuchid *Gracilisuchus stipanicicorum* (Romer, 1971, 1972a). A partially articulated pectoral extremity that comprises scapula, humerus, radius, and ulna, is present on the same side of the slab, but is not directly associated with the axial and hind limb elements of the *Lagosuchus* holotype. These forelimb elements are badly preserved, deformed and incomplete, and can only be examined from one side, due to the state of preparation. Romer (1971, 1972a) expressed no doubts that the forelimb and hind limb elements belong to the same individual. However, since these finds are part of a multi-taxon death assemblage, there is no positive evidence for this assumption (Sereno and Arcucci, 1994). Sereno and Arcucci (1994) also regard the holotypic skeleton of *Lagosuchus talampayensis* as non-diagnostic, rendering the name a *nomen dubium*.

Romer (1972a) erected a second species of *Lagosuchus*, *L. lilloensis,* for the newly found specimen PVL 3871, which is about 50% larger than *L. talampayensis*. Originally, the specimen included no forelimb material (Romer, 1972a:5). Bonaparte (1975) attributed new Los Chañares material to *Lagosuchus*, rejected Romer's (1972a) interpretation of the larger specimen as a second species, and listed under PVL 3871 a left scapulocoracoid, humerus, radius, and ulna, without explaining where this material was found or why these elements were not mentioned by Romer. Furthermore, Romer (1972a) described an isolated scapulocoracoid ('MCZ 4121', now labeled MCZ 9483) and referred it to *Lagerpeton*. However, this specimen is also figured in Romer's work, and the figure caption as well as the label in the MCZ collection refers it to *Lagosuchus talampayensis*. Anyway, this element was found isolated from the other partial skeletons (Romer, 1972a), rendering any referral doubtful. Finally, Sereno and Arcucci (1994) transferred the entire *Lagosuchus* hypodigm (with the exception of MCZ 9483, which was not mentioned by these authors) to the new genus *Marasuchus*. PVL 3871 was declared as the holotype, and new material was assigned to this genus, including a partial vertebral column (PVL 4672). Under this number, the PVL collection catalogues also a right scapulocoracoid and humerus. However, these elements were not mentioned or described by Sereno and Arcucci (1994), leaving the origin and possible association with other Los Chañares findings unclear. In summary, there is not a single forelimb element that can be confidently referred to *Marasuchus lilloensis*, a conclusion that is supported by the unusual morphology of the forelimb elements catalogued under PVL 3871 (see section 'Anatomy' below).

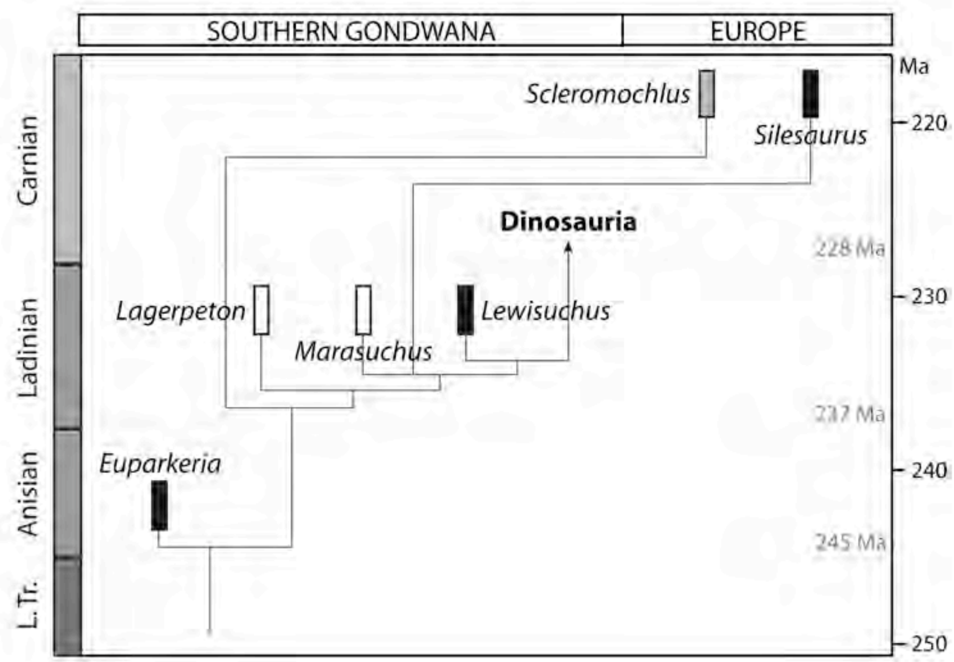

Figure 4-1. Stratigraphic and spatial distribution of *Euparkeria* and basal Ornithodira. Black bars indicate taxa with preserved forelimb material, white bars stand for taxa that lack forelimb material. The forelimbs of *Scleromochlus* are badly preserved (see text for details). Cladogram based on Benton (2004).

Lewisuchus admixtus was erected and described by Romer (1972b) and only recently recognized as a member of Dinosauriformes (Arcucci, 1997). The type material PVLR 01 (formerly MLP 64-XI-14-14; Romer, 1972b) consists of an articulated skeleton that comprises both scapulocoracoids, the left humerus, and fragments of the left forearm. The left part of the shoulder girdle and humerus are still articulated with the skeleton and partially embedded in matrix, but the right scapulocoracoid has been prepared off the slab and can be examined from all sides. In Hutchinson's (2001a) consensus cladogram, *Lewisuchus* is more closely related to Dinosauria than other dinosauriforms, probably based on the analysis of Novas (1996) and Arcucci's (1997) assumption that *Pseudolagosuchus* might be a junior synonym of *Lewisuchus*.

Finally, remains of another dinosauromorph, *Silesaurus opolensis*, were found in the Late Carnian Krasiejów claystone of southern Poland (Dzik, 2003). Among many isolated bones, four partially articulated skeletons were extracted from the rock. Three of these specimens also comprise forelimb material (scapulocoracoids, humeri, radii, ulnae), but all elements are still partially embedded in matrix. Unfortunately, *Silesaurus* could not be examined during this study, and no photographs of the postcranial material were published. Thus, the comments on the forelimb anatomy of *Silesaurus* below are based on the short description and figures published by Dzik (2003). Moreover, Dzik (2003) puzzled about the combination of plesiomorphic and advanced characters that can be seen in the material, but did not perform a cladistic analysis. Therefore, the phylogenetic position of the new taxon is currently unsure, despite some shared derived characters with Dinosauriformes. Drawing conclusions based on this form regarding dinosaur forelimb evolution is hence difficult.

Another species attributed to Dinosauriformes, *Agnostiphys cromhallensis,* was extracted from Upper Triassic fissure deposits in southwest England (Fraser et al., 2002). However, all elements, including a right humerus, were found unarticulated in a bonebed. This hampers a reliable reconstruction of this form, which will therefore not be considered in the following discussion.

In summary, the picture of the beginnings of dinosaur forelimb evolution is rather patchy. The Anisian form *Euparkeria* may serve as the starting point for the evolution of both Crurotarsi and Ornithodira. However, in the Ladinian forms from the Los Chañares Formation, no reliable information on forelimb anatomy is preserved, with the exception of *Lewisuchus*. Due to their late appearance in the fossil record, the Late Carnian forms *Scleromochlus* and *Silesaurus* are obviously representatives of specialized lineages that evolved independently for at least 10-15 Ma (fig. 4-1). In contrast to the Ladinian dinosauriforms and the first dinosaurs of the Carnian, these taxa were found in the northern hemisphere, adding also a spatial gap to the origin of dinosaurs. Considering their debated phylogenetic position, these forms may not serve as good models for the dinosauriform *bauplan* that gave rise to Dinosauria. Therefore, only *Euparkeria* and *Lewisuchus* form the base for an evaluation of the beginnings of dinosaur forelimb evolution, making a detailed reexamination of the anatomy of these taxa necessary.

Anatomy

Basal Archosauria: *Euparkeria capensis*

Euparkeria capensis is a comparatively small animal, having roughly the size of a cat. The shoulder girdle is relatively massive, with large coracoids that almost meet in midline, separated only by a spatulate interclavicle. Long, sigmoidal clavicles are placed cranially to these elements and meet in midline at the tip of the interclavicle (fig. 4-2).

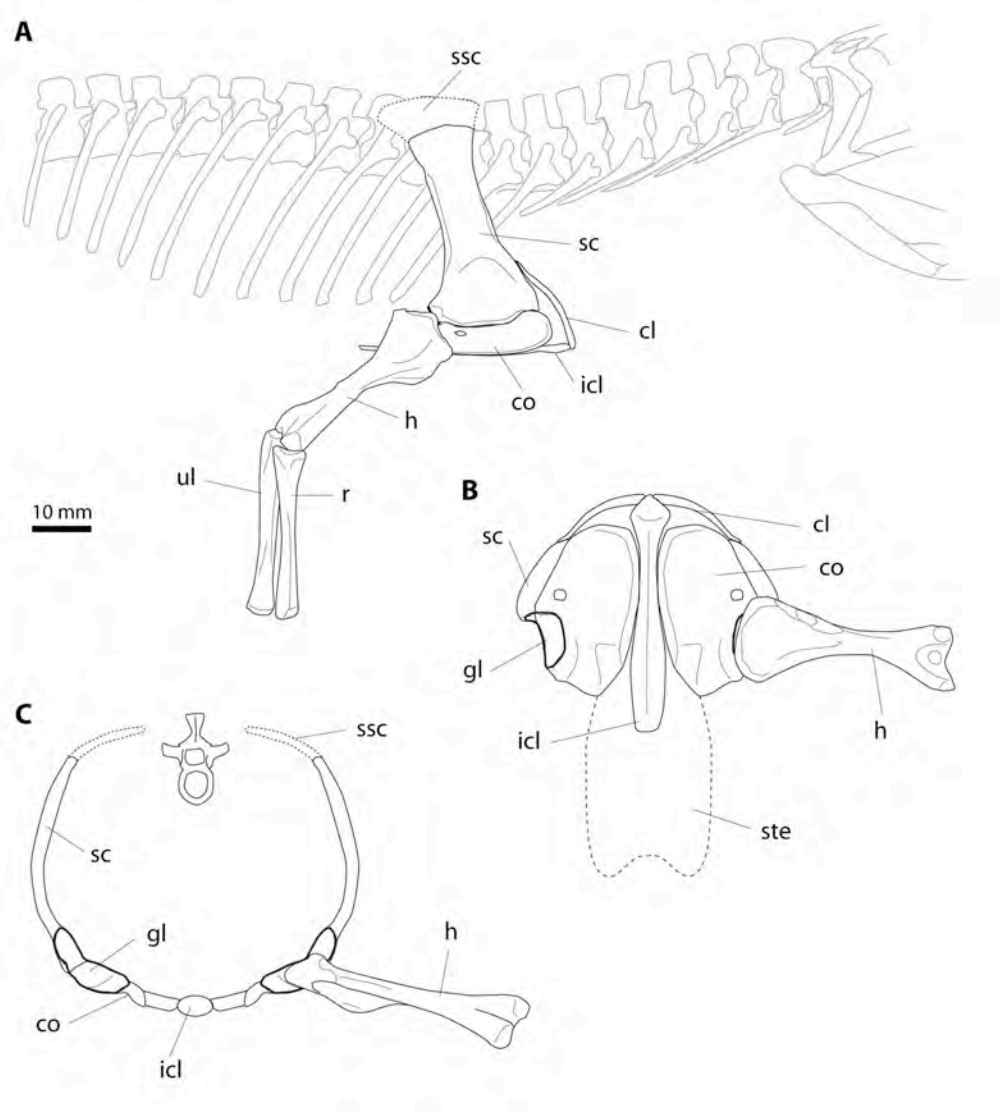

Figure 4-2. Reconstruction of the shoulder girdle of *Euparkeria capensis*. A, lateral view; B, ventral view; C, caudal view. The cranial and axial skeletal elements are schematically drawn.

Scapulocoracoid. The elongate scapula (fig. 4-3) has a broad and straight shaft that is not much constricted at its base, making its cranial and caudal borders oriented in parallel. The shaft is inclined caudally relative to the vertical with about 20°, and is only slightly expanded at its distal end. The expansion is caudally more pronounced than cranially. The cranial and caudal parts of the distal expansion are flattened, while the center is slightly convex in craniocaudal direction. The cranial edge of the scapular blade is sharp in its distal two thirds, but becomes rounded in the ventral third. The caudal edge is thickened and rounded, especially in the ventral third of the blade. The central part of the lateral face of the scapula blade is flat and shows no differentiation into cranial and caudal facets. On its medial side, the shaft is concave ventrally, and flat dorsally. As already pointed out by Ewer (1965), the shaft of the scapula is striated in dorsoventral direction, both laterally and medially.

In caudal view, the scapular head is deflected about 50° ventrolaterally relative to the shaft. The lateral side of the head of the scapula is concave, but in contrast to many dinosaurs, there is no acromial crest bordering this depression dorsally. The concavity is triangular in outline, extending with its tip onto the base of the shaft. The dorsocranial edge of the head (the acromial region, *sensu* Howell [1936a] and Romer [1956]) is thickened and rounded, separating the lateral concavity from the border of the bone. On the supraglenoidal area, there is flattened and roughened facet that may extend over the ventral third of the caudal side of the scapula (SAM 7700). A rugose tubercle projects laterally at the dorsal glenoid border, caudodorsally to the scapulocoracoidal suture. The suture is straight in its caudal half, but curves cranioventrally towards the cranial edge of the scapulocoracoid. Medially, the scapular head is concave in its center, but the glenoidal and acromial regions are convex. Immediately cranial to the supraglenoidal buttress, a narrow groove leads ventrally towards the coracoid foramen.

The scapular part of the glenoid is wider than long and caudoventrally oriented, while the elongate coracoidal part is larger than the former, longer than wide, and caudolaterally oriented. Both facets are slightly concave.

The coracoid of *Euparkeria* is best preserved in specimen SAM 6047. It has an oval outline, being longer craniocaudally than wide transversally, and straight medial and lateral edges (fig. 4-3). The external (ventral) surface is slightly convex transversally, the internal (dorsal) surface strongly concave. However, the ventral surface bears two oval fossae directly medial and cranial to the glenoid, separated from each other by a slight swelling (which is more enhanced in SAM 5867). The cranial fossa exhibits a sharp edge along its cranial border. The glenoid connects to the cranial fossa by a wide recess. Another slight depression is situated along the medial edge of the coracoid. A bulging glenoid lip separates the glenoid from the subglenoid fossa. The caudomedial edge of the coracoid is thickened and dorsally deflected, and probably served for articulation with the cartilaginous sternum. Between the depression along the medial border and the subglenoid fossa, craniolaterally oriented striations indicate muscle attachment. The large, oval coracoid foramen is craniomedially oriented and situated about midlength, close to the sutural line. The cranial part of the coracoid, which exhibits radial striations, is thin-walled, but its craniomedial edge is somewhat strengthened. The sutural facet for the scapula is relatively flat, but exhibits a slight concavity in its cranial part.

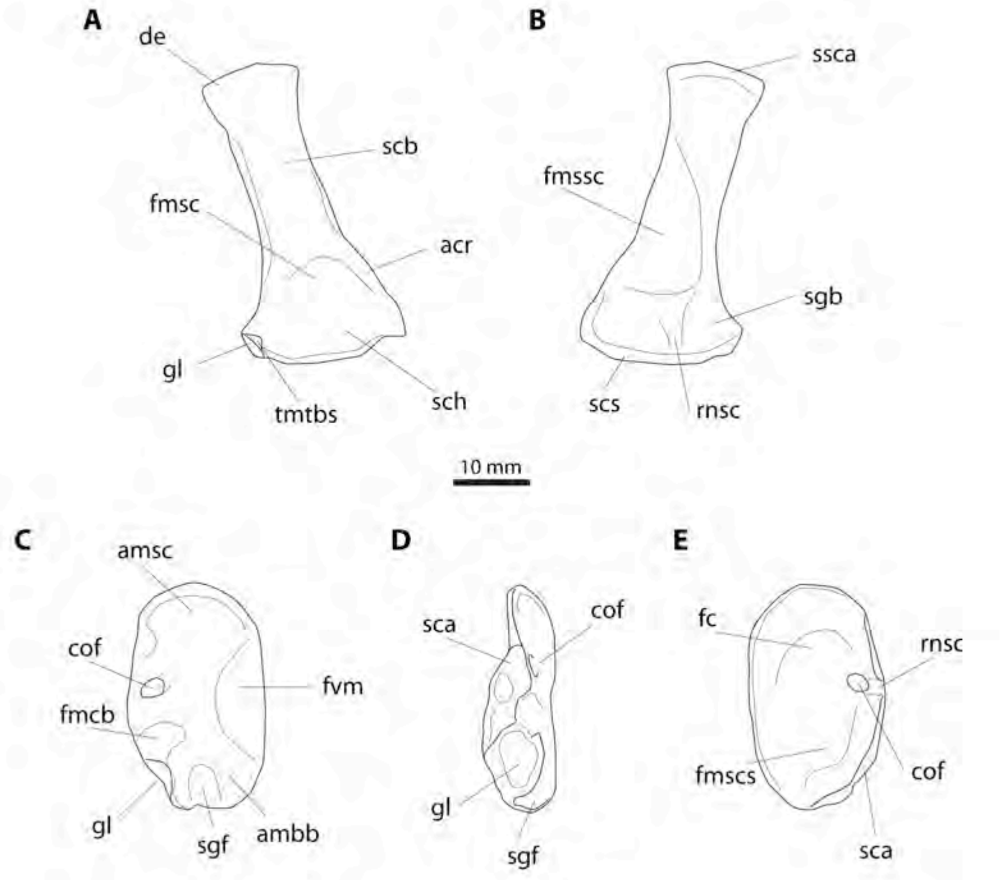

Figure 4-3. Osteological structures of the pectoral girdle elements of *Euparkeria,* based on SAM 6047 (mirrored). Scapula in lateral (A) and medial (B) views. Coracoid in ventral (C), lateral (D), and dorsal (E) views.

Interclavicle and clavicles. The elongate, dorsoventrally flattened interclavicle has a transversely slightly convex ventral side. Its cranial part appears to be widened and lozenge-shaped in the holotype, but Ewer (1965) did not describe this feature. As Ewer (1965) already mentioned, the interclavicle is striated longitudinally, probably due to dermal sculpturing.

Only fragments of the clavicles are preserved in the holotype, but their form can be inferred from natural molds in the matrix. The clavicles are slightly sigmoidal and have a round cross-section. The apical end is craniocaudally flattened for articulation with the scapula.

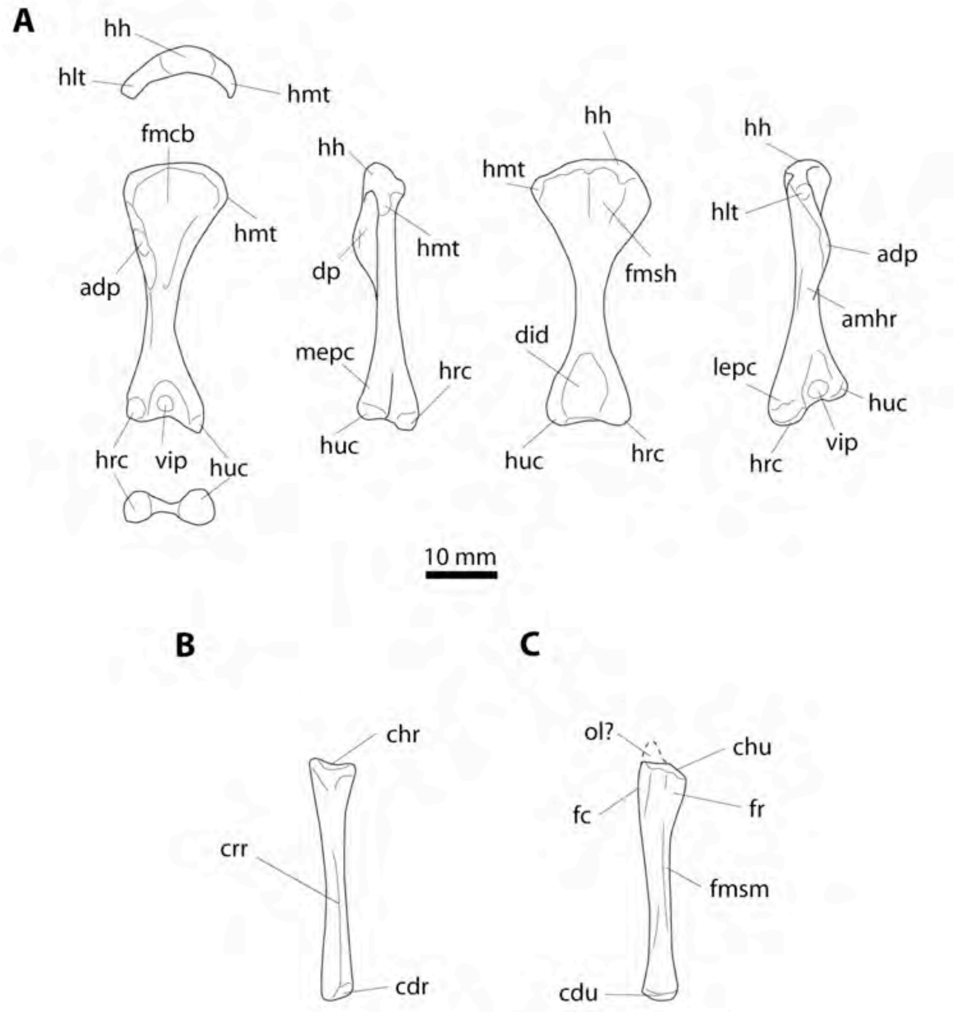

Figure 4-4. Osteological structures of the forelimb elements of *Euparkeria.* A, humerus in (from left to right) proximal, ventral, distal, caudal, dorsal, and cranial views (based on SAM 7700, mirrored). B, radius, and C, ulna, in cranial views (as preserved in SAM 5867).

Humerus. In the holotype (SAM 5867), the slender humerus (fig. 4-4) is exposed from its ventral side only, but other specimens (SAM 6048, 7696, 7700) allow for an examination from all sides. The deltopectoral crest has a triangular outline with a ventrally directed, slightly rugose apex, and extends distally along the proximal third of the humerus. Both the proximal and the distal ends of the humerus are expanded. On the ventral side of the proximal expansion, there is a wide triangular depression that extends distally up to the distal end of the deltopectoral crest. The medial tuberosity is dorsoventrally deep, has an oval shape and is flattened caudally. In proximal view, it is deflected ventrally relative to the axis of the humeral head at about 30°. Cranially, the thickened proximal base of the deltopectoral crest is ventrally deflected at a similar angle. The diaphysis has an oval to subtriangular cross-section, the craniocaudal axis being longer than the dorsoventral axis. The dorsal face of the humerus is subdivided proximally into three shallow, subtriangular facets that are separated from each other by low ridges. The humeral head extends only slightly onto the dorsal side, and is bordered by another small facet medially. Dorsodistally to the medial tuberosity, there is a prominent, subcircular scar. Further distally, the dorsal side of the humerus becomes smooth and slightly convex in craniocaudal direction. The distal humeral expansion is twisted about 40° cranioventrally relative to the axis of the proximal expansion. The radial condyle is slightly smaller than the ulnar condyle. Both condyles have a hemispherical shape in distal view, and are separated by a wide intercondylar depression. The intercondylar depression on the ventral face of the distal expansion is oval in outline, and exhibits a distinct circular pit on its distal end. On the dorsal side of the distal expansion, there is a wide, triangular depression.

Antebrachium. Radius and ulna are both slender, elongate bones in *Euparkeria*, but do not surpass the humerus in length. The radius has a subcircular cross-section, the craniocaudal axis being somewhat longer than the transverse axis. The surface of the shaft is smooth, and shows no intermuscular ridges or striations. Proximally, the humeral cotyle is circular and concave. About 2 mm distal to the articular facet, a small tubercle projects medially. The distal expansion has an oval outline (the long axis being transversely oriented) and is distomedially deflected. On its caudolateral side, there is a shallow fossa that receives the articular process of the ulna.

No olecranon process can be observed on the ulna, because that part of the bone is still embedded in the matrix. The caudolateral face of the proximal end of the ulna is transversally rounded and roughened. There is no distinct lateral process, but a narrow ridge that extends distally for one-fifth of the bone. The distal half of the lateral side of the ulnar shaft is flattened, and is cranially bordered by a sharp intermuscular ridge. Distally, the articular expansion exhibits a low tubercle cranially that serves for articulation with the radius. The articular facet is transversally widened and only slightly convex. Since they are still embedded in matrix, the medial and caudal sides of the ulna cannot be examined.

Manus. Ewer (1965) reported the presence of metacarpals I to IV plus the first phalanx of digit I in specimens SAM 13666 and 13667. These elements could not be located during the collection studies by the author; hence, a brief summary of Ewer's (1965) description is given here. The manus of *Euparkeria* is characterized by a stout metacarpal I that is only half as long as metacarpal II. The distal condyles of metacarpal I are asymmetric, and the first phalanx of digit I is short and block-like. Metacarpal II is robust, while metacarpals III and IV are slightly more slender and somewhat shorter. Judging from Ewer (1965:fig. 10i), the hand of *Euparkeria* already had a structure like that of *Eoraptor* and other basal dinosaurs (see chapter 5).

Basal Dinosauriformes: *Lewisuchus admixtus*

The holotype of *Lewisuchus admixtus* (PVLR 01) has about the same size as *Euparkeria*, but scapula and humerus are more slender and elongate (fig. 4-5). Moreover, the coracoid is relatively reduced in size. Scapula and coracoid are completely co-ossified, showing no sutural line.

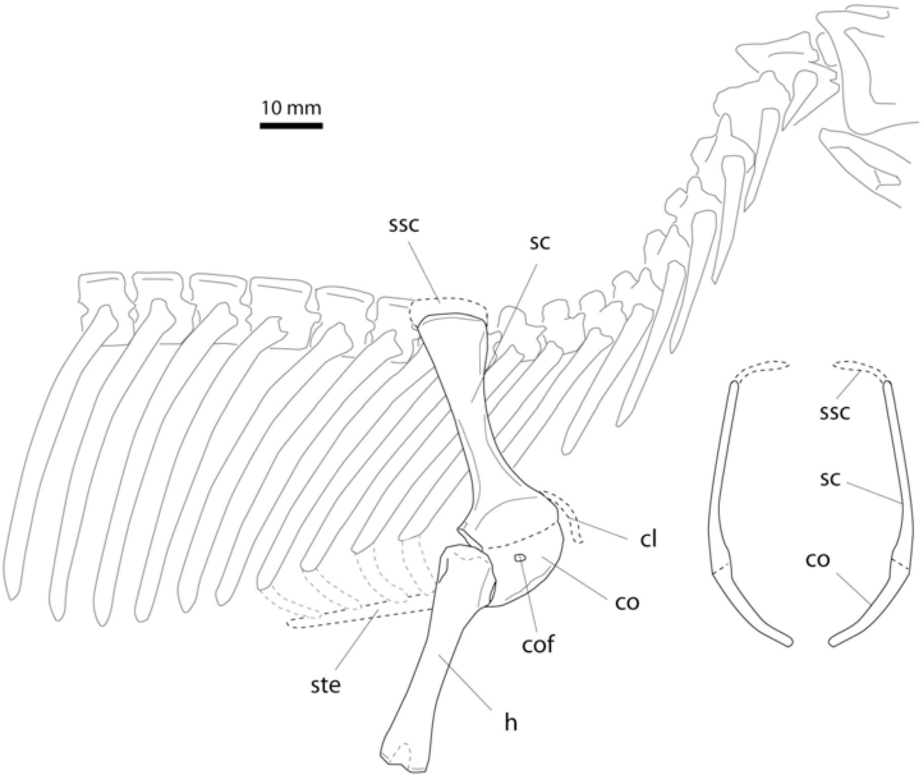

Figure 4-5. Reconstruction of the pectoral girdle of *Lewisuchus admixtus* (PVLR 01). Dashed lines indicate inferred bony and cartilaginous elements that are not preserved. The cranial and axial skeletal elements are based on *Marasuchus* (Sereno and Arcucci, 1994) and schematically drawn. On the right side, a reconstruction of the profile of the pectoral girdle is shown in cranial view.

Scapulocoracoid. The scapular blade is elongate and considerably constricted at its base (fig. 4-6). Distally, the blade significantly expands cranially, rendering its cranial border distinctly curved, while the caudal border remains straight. Proximally, the caudal border exhibits an elongate facet. In the cranioproximal area of the blade, there is a faint semilunate depression that has a rugose surface texture. The lateral side of the distal expansion is flattened and bears a triangular facet cranially. Both the cranial and the caudal edges of the scapular blade are sharp. Proximally, the medial side of the blade exhibits an elongate supraglenoidal swelling at the cranial border of its caudal third, rendering the cross-section of the base of the blade lozenge-shaped. Distally, the swelling ends at a craniocaudally oriented ridge. The distal part of the medial side of the blade is flattened.

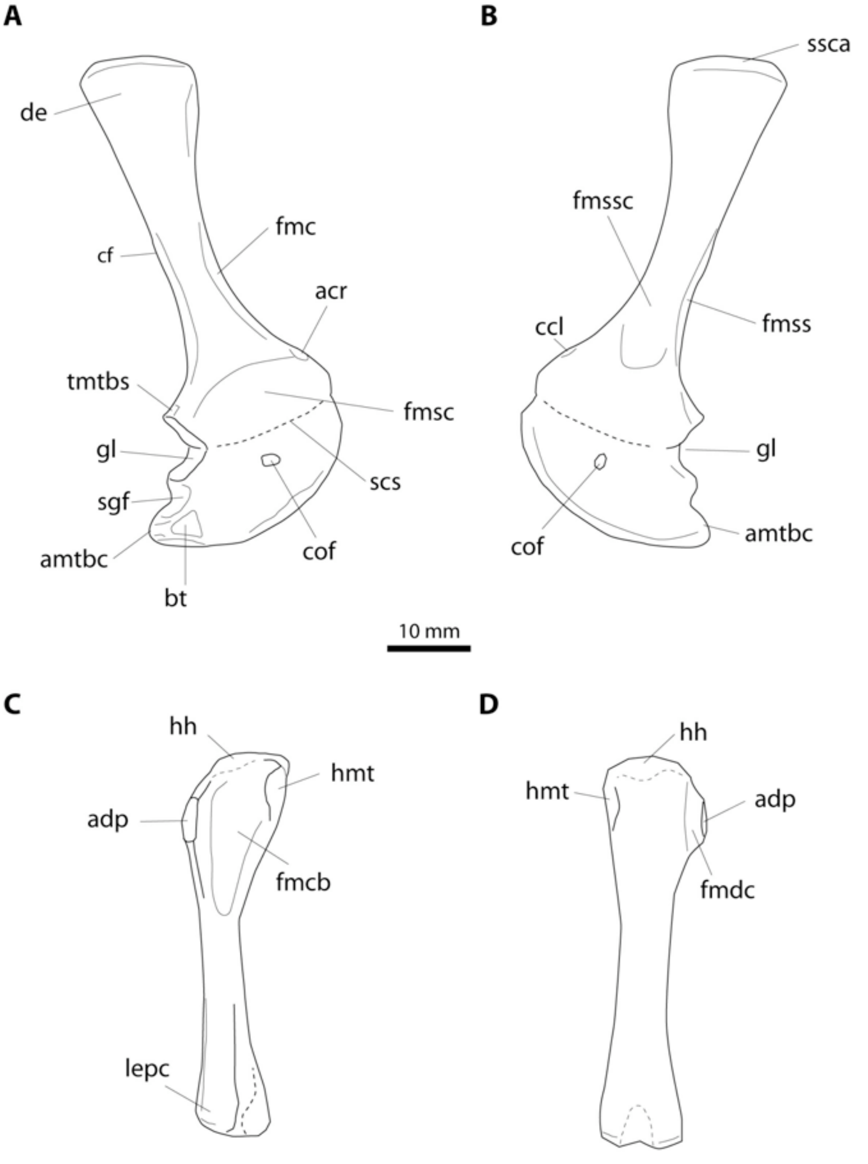

Figure 4-6. Osteological structures of the forelimb elements of *Lewisuchus* (PVLR 01). Scapulocoracoid in lateral (A) and medial (B) views, humerus (mirrored) in ventral (C) and dorsal (D) views.

In comparison to the shaft, the scapular head is relatively small. Ventrolaterally, a deep fossa extends over the entire craniocaudal width of the scapular head. This fossa is bordered dorsally by a smooth swelling and lacks a distinct acromial ridge. The acromial region of the scapular head exhibits a laterally oriented, oval tubercle that has a slightly roughened surface. On the cranial edge next to this tubercle, there is a small, triangular articular facet for the clavicle. Caudally, the glenoid is bordered dorsally by a small, laterally projecting ridge. The caudal side of the head dorsal to the glenoid is wide, flattened, and ends at a sharp ridge laterally. Medial to this ridge, there is an elongate scar, but no distinct tubercle as in *Euparkeria*. An oblique, caudoventrally running ridge subdivides the dorsomedial side of the scapular head into two oval depressions, one situated craniomedially, the other caudolaterally.

Both the scapular and coracoidal parts of the glenoid are rectangular and caudolaterally directed. There is no clear glenoid lip, neither dorsally nor ventromedially. The articular facets of both parts of the glenoid are flat.

The coracoid (fig. 4-6) has an elongate, oval outline. Its cranial and medial borders are relatively wide, rounded and rugose. Caudomedially, there is a large, lozenge-shaped tubercle that is posteroventrally directed. Its ventromedial side exhibits a smooth facet. Dorsomedial to this tubercle, an elongate, comma-shaped, caudolaterally oriented depression extends to the glenoid rim. This depression is bordered by a narrow ridge caudomedially and by a small tubercle ventromedially. A large, triangular tubercle with a rugose surface texture (for the attachment of M. biceps brachii, see below) is adjacent cranially. Starting at this tubercle, a smoothly rounded ridge extends cranially and divides the ventrolateral face of the coracoid into a dorsolateral and a ventromedial part. The dorsolateral part of the coracoid is flat and smoothly merges with the fossa on the scapula head. The ventromedial part is relatively narrow and sickle-shaped. The coracoid foramen is circular and appears to be more ventromedially placed than in *Euparkeria*. In dorsomedial view, the coracoid is strongly concave.

Humerus. The humerus of *Lewisuchus* is very slender, but the proximal end is damaged and parts of the distal end are broken off (fig. 4-6). Therefore, the outward rotation of the distal end relative to the proximal expansion is hard to estimate, but is in the range of 30-45°. Proximally, the main part of the humeral head is not preserved, but its base is still visible on the dorsal side of the humerus. Obviously, the head significantly extended dorsally. The medial tuberosity has a pointed, triangular outline in proximal view and exhibits a large tubercle on its dorsal face. It is not deflected relative to the main axis of the proximal expansion. The deltopectoral crest is relatively low and has a smoothly rounded outline, the apex being situated midway of its proximodistal extent. The crest extends distally about two fifths of the total humeral length. In ventral view, the ventrally oriented apex is spindle-shaped and projects both medially and laterally beyond its base. The ventral side of the proximal expansion exhibits a large, oval concavity that extends onto the medial side of the deltopectoral crest. The adjacent ventral face of the humeral shaft is flattened, the cranial and caudal sides are rounded. On the lateral side of the deltopectoral crest, there is a longitudinal groove between the overhanging apex and a proximodistally running ridge on the craniodorsal edge of the humerus. The dorsal aspect of the proximal expansion exhibits a shallow, elongate depression between the medial tuberosity and the humeral head, and a smooth facet directly distal to the humeral head. The remaining surfaces of the humerus are still embedded in matrix and cannot be examined.

Comments on other forms

Other basal dinosauriforms may contribute to our understanding of the forelimb anatomy of this group, but due to doubtful associations, bad preservation or unresolved phylogenetic positions (see section 'data quality' above), the morphology of the forelimb elements referred to *Lagosuchus*, *Marasuchus*, and *Silesaurus* will only briefly be compared to *Lewisuchus* here.

The holotype of *Lagosuchus talampayensis* (PVLR 09) preserves only the proximal part of the scapula. Despite the poor state of preservation, it can be recognized that the base of the scapular shaft is craniocaudally constricted. Moreover, its cranial border is curved and its caudal border straight. Therefore, the scapula appears to be of a type similar to that of *Lewisuchus*. The humerus is more slender and elongate than in *Lewisuchus*, and the small, triangular deltopectoral crest is restricted to the proximal quarter of the bone. Like in *Euparkeria,* radius and ulna are slender, but relatively short in comparison to the humerus. The proximal end of the ulna exhibits no olecranon process.

Among the elements referred to *Lagosuchus talampayensis* by Romer (1972a), the scapulocoracoid MCZ 9483 closely resembles that of *Lewisuchus*, but it is about 25% smaller and exhibits different proportions. There are also minor differences in the form of the distal expansion of the scapula blade, the shape of the fossa on the scapular head, the strength of the glenoid lips, and the form of the biceps tubercle on the coracoid. Therefore, it can be concluded that MCZ 9483 probably belongs to a closely related dinosauriform, but not to *Lewisuchus admixtus*.

The scapulocoracoid and forelimb elements catalogued under PVL 3871 (the holotype of *Marasuchus lilloensis*) are entirely different from that of *Lewisuchus* and MCZ 9483. The scapula blade is short, stout and has an enormous distal expansion that also extends caudodorsally; the glenoid projects caudally and has subcircular articular surfaces; the humerus is extremely long and slender, its proximal end is only slightly and its distal end almost not expanded; the deltopectoral crest extends only about one third down the shaft. Bonaparte (1975) described these elements in detail, and noted similarities of the humerus to the corresponding element of the sphenosuchians *Hesperosuchus* and *Pseudohesperosuchus*. Similarities to basal crocodylomorphs were also recognized by Sereno and Arcucci (1994). The form and proportions of the scapulocoracoid, radius, and ulna closely correspond to Sphenosuchia, too (fig. 4-7; compare also to Huene, 1921:fig. 12; Bonaparte, 1971:figs. 28–30; Crush, 1984:fig. 7; Walker, 1990:figs. 40, 42, 43; Clark et al., 2000:fig. 3; Sues et al., 2003:fig. 3; Clark et al., 2004:fig. 3). Considering that Romer (1972a) did not mention the presence of forelimb material in the holotype of *Marasuchus lilloensis*, it is concluded here that these elements are sphenosuchian in origin, and were accidentally added to the *Marasuchus* type material by Bonaparte (1975).

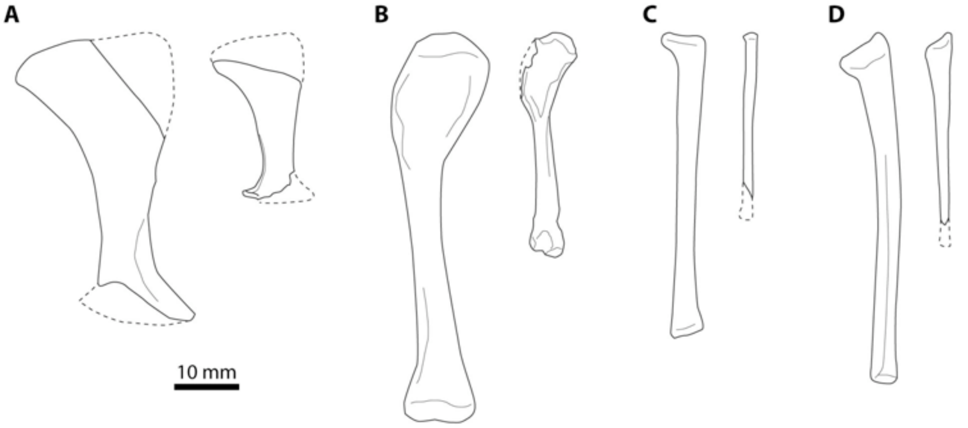

Figure 4-7. Comparison between forelimb elements (A, scapula; B, humerus; C, radius; D, ulna) of *Hesperosuchus agilis* (CM 29894, left) and those referred to *Marasuchus lilloensis* (PVL 3871, right). Aside from size differences, the elements are virtually identical. *Hesperosuchus* elements are redrawn after Clark et al. (2000).

The second scapulocoracoid and humerus of unclear origin, PVL 4672 (labelled with *Lagosuchus*), differ considerably from the corresponding elements of *Lewisuchus* and MCZ 9483. However, they are also unlike the sphenosuchian forelimb elements catalogued under PVL 3871. Like in basal sauropodomorphs, the scapular blade is relatively short, and its distal expansion projects both cranially and caudally (chapter 6). The coracoidal part of the glenoid is elongate and has almost double the size of the scapular part, resembling the basal saurischian

Eoraptor in this respect (chapter 5). However, PVL 4672 is not well preserved, which makes a reliable determination of its systematic affinities difficult.

The forelimb elements of *Silesaurus opolensis,* as figured by Dzik (2003), are unusual in shape. The scapular blade resembles that of *Lewisuchus* in its slenderness, and in the presence of a curved cranial and a straight caudal edge. The glenoid is also similar in shape, but the ventromedial part of the coracoid appears considerably compressed. Humerus, radius, and ulna are extremely elongate and slender, making the forelimb only slightly shorter than the hind limb. In Dzik's (2003) figures, no surface features of the long bones can be recognized. The humerus even seems to lack a deltopectoral crest. It is obvious that *Silesaurus* was a highly specialized form, also with respect to the forelimbs. The significance of these adaptations have to remain unclear until the phylogenetic position of this taxon can be determined more precisely. Interestingly, the basal ornithodiran *Scleromochlus taylori* exhibits a similar elongation of humerus and antebrachium, but its forelimb remains significantly shorter than the hindlimb (Benton, 1999).

Muscle reconstructions

With the review of reptilian forelimb muscles and the discussion of phylogenetic inferences for the last common ancestor of all archosaurs as a basis (chapter 3), it was possible to reconstruct muscle attachment sites in *Euparkeria* (figs. 4-8, 4-9) and *Lewisuchus* (fig. 4-10). Some muscles can be localized easily, others must have been present but the extent of their attachments can hardly be delimited. For others again, phylogenetic inference and bone morphology provides equivocal results only, rendering their reconstruction a matter of speculation.

Euparkeria

The smooth, undivided lateral surface of the scapular blade of *Euparkeria* (fig. 4-8A) makes a definite delimitation of attaching muscles impossible. Considering their distribution in other non-avian reptiles, M. deltoideus scapularis, M. scapulohumeralis cranialis, and M. scapulohumeralis caudalis must have been present, but no clear facets or intermuscular ridges indicate their borders. The presence of M. teres major is equivocal, since the muscle exists in archosaurs but not in other diapsids. Because the lateral face of the scapular blade shows no differentiation into cranial and caudal facets, this muscle in *Euparkeria* may not have evolved yet, and is therefore not included in the reconstruction presented here. As in all non-avian reptiles, M. levator scapulae would have attached to the cranial edge of the blade. The thickening of the cranial border in its ventral third, accompanied by a narrow facet on the adjacent lateral side of the blade, probably correlates to the insertion of M. cucullaris. The elongate, caudolaterally oriented facet along the caudal border of the blade possibly indicates the attachment of a superficial layer of M. serratus superficialis, which attaches to the caudal edge of the scapular blade in extant non-avian reptiles (chapter 3). A similar facet is found on the medial side of the blade, probably correlating to a ventral layer of this muscle. The large, triangular depression laterally on the scapular head probably served for the attachment of M. supracoracoideus pars scapularis. No other muscle is known to attach in this area in extant Reptilia (chapter 3). Cranial to this fossa, the widened acromial area would make an accessory attachment of M. deltoideus clavicularis possible, but no surface texturing that would indicate muscle attachment can be recognized in this region. Caudolaterally, the tubercle that neighbors the glenoid unambiguously correlates to M. triceps brachii caput scapulare, like in all diapsids (chapter 3). On the medial side of the scapular blade (fig. 4-8B), the triangular depression probably correlates to the origin of the scapular head of M. subcoracoscapularis. The origin of M. serratus profundus distally is hard to delimit, but longitudinal striations close to the distal rim indicate an attachment of this muscle on the bony scapula.

On the ventral side of the coracoid (fig. 4-8C), the subglenoid fossa would have served for the insertion of M. costocoracoideus, considering the topology of this muscle in other Reptilia (chapter 3). The oval, striated area that medially neighbors the subglenoid fossa probably represents the homologue of the large tubercle that projects from this area in Ornithodirans, and would have served for the origin of M. biceps brachii. The sharply bordered fossa cranial to the glenoid probably served for the attachment of M. coracobrachialis. However, this muscle covers a large portion of the coracoid in extant non-avian diapsids (chapter 3), and possibly extended medially beyond this fossa. It cannot be determined if also the depression along the medial border of the coracoid is correlated to M. coracobrachialis, or if this depression may have accommodated a lateral extension of the attachment of M. pectoralis along the interclavicle. In figure 4-8C, the latter model is depicted. Since there is no tubercle or flange on the caudal edge of the scapula that would indicate the attachment of the Ligamentum sternoscapulare internum (which would correlate to a crocodilian-like M. triceps brachii caput coracosternale [chapter 3]), it is assumed here that *Euparkeria* preserved the plesiomorphic configuration of the coracoidal head of M. triceps brachii. Therefore, a tendinous origin of this muscle is reconstructed on the caudal edge of the coracoid. On the medial side of the coracoid, the central concavity probably correlates to the origin of the coracoidal part of M. subcoracoscapularis, which must have been present in non-crurotarsan archosaurs (chapter 3). Moreover, at least one M. sternocoracoideus probably attached to the cranial region of the coracoid, like in basal diapsids (chapter 3).

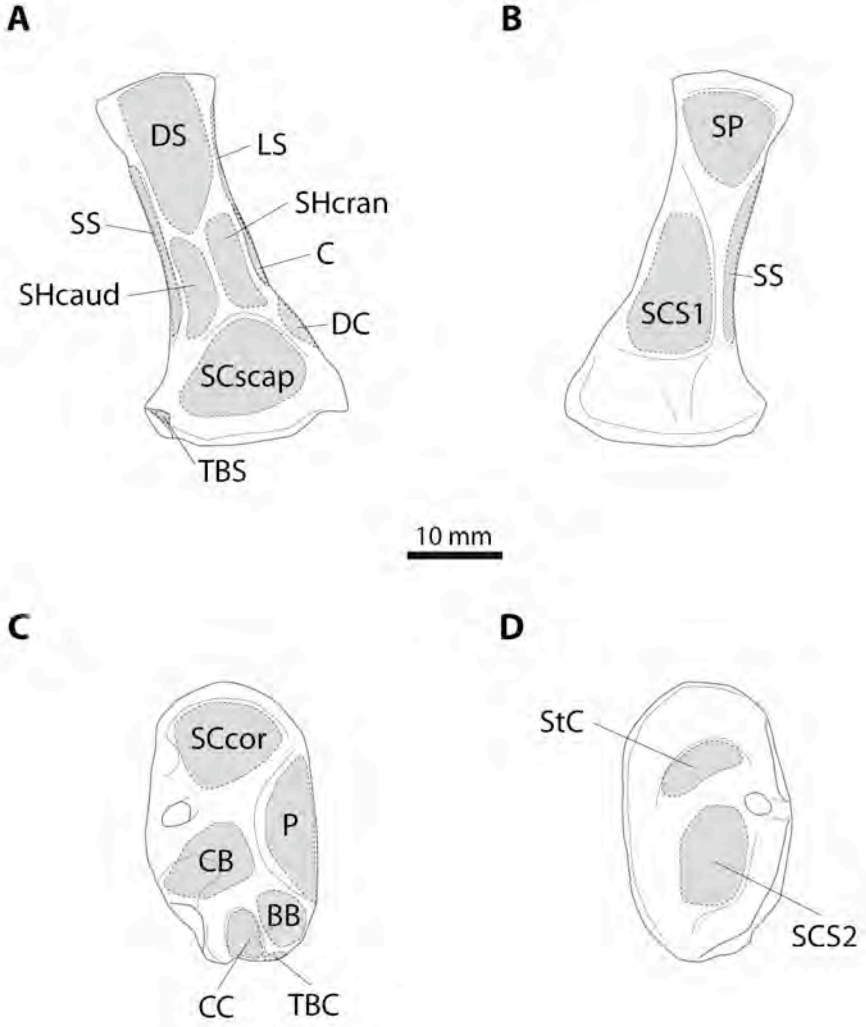

Figure 4-8. Reconstruction of muscular attachments on the scapula (A, lateral view; B, medial view) and coracoid (C, ventral view; D, dorsal view) of *Euparkeria*. For explanations see text.

The triangular depression on the proximal part of the ventral side of the humerus (fig. 4-9A) probably served for the insertion of M. coracobrachialis, like in all tetrapods (chapter 3). Other unambiguous muscular attachments on the humerus include that of M. supracoracoideus (apex of the deltopectoral crest), M. subcoracoscapularis (medial tuberosity), M. pectoralis (caudal side of the deltopectoral crest), and M. deltoideus clavicularis (cranial side of the deltopectoral crest). A number of other muscles that attach to the humerus cannot be delimited so clearly, although phylogenetic inference implies they were present. These include the two humeral heads of M. triceps brachii, the position of which can only be roughly estimated since there are no osteological correlates. The insertions of M. latissimus dorsi (as indicated by the subcircular scar dorsally on the humerus) and M. scapulohumeralis cranialis plesiomorphically are situated between these two heads of M. triceps brachii (chapter 3). Thus, a similar configuration is reconstructed here for *Euparkeria* (fig. 4-9A). Like in other diapsids, M. scapulohumeralis caudalis probably inserted caudoproximally on the humerus, but its extent and relations to M. triceps brachii caput humerale mediale and M. scapulohumerals cranialis are speculative. On the dorsocranial side of the proximal humerus, the insertion of M. deltoideus scapularis is not easy to identify. This muscle possibly inserted on the proximal cranial face of the deltopectoral crest, as in other non-avian reptiles (chapter 3). However, the distinct tubercle on the cranioproximal corner of the humerus may also be correlated to muscle attachment, and no other muscle than M. deltoideus clavicularis attaches in this region in extant diapsids. M. humeroradialis, which is prominent in crocodilians but minute or lost in other tetrapods, was probably also present in *Euparkeria*. Like in extant forms, the sharp ridge dorsodistally to the deltopectoral crest indicates its origin and separated it from M. triceps brachii caput humerale laterale. M. brachialis is inferred to have arisen from the cranioventral humeral shaft, but no osteological correlates help to delimit its extent. The reconstructed configuration of the muscles that attached to the epicondyles is based on the corresponding patterns in *Alligator* and *Sphenodon*, but remains speculative due to the lack of unambiguous correlates on the bone. However, this uncertainty has not much effect on the resulting lines of action (see below).

The facets that are visible on the exposed sides of radius and ulna allow for a reconstruction of M. supinator manus. This muscle apparently had developed a radial attachment, as indicated by a faint cranial intermuscular ridge on the distal half of the bone. Phylogenetic inference implies that the medial side of the radius served for the origin of M. supinator, while the craniolateral face of the ulna was covered by M. ectepicondylo-ulnaris (chapter 3). M. abductor radialis probably attached to the proximal part of the lateral side of the radius, but there is no clear demarcation against the origin of M. supinator manus. Between M. abductor radialis and M. supinator, the laterally projecting tubercle possibly represents the point of attachment of M. humeroradialis. The insertion of that muscle is correlated with a distinct tubercle in crocodilians, too (chapter 3); however, it is more medially placed in extant forms. The rugose area distal to the olecranon process on the ulna of *Euparkeria* probably represents the area of attachment of the connective tissue of the elbow joint, in prolongation of the tendon of insertion of M. triceps brachii.

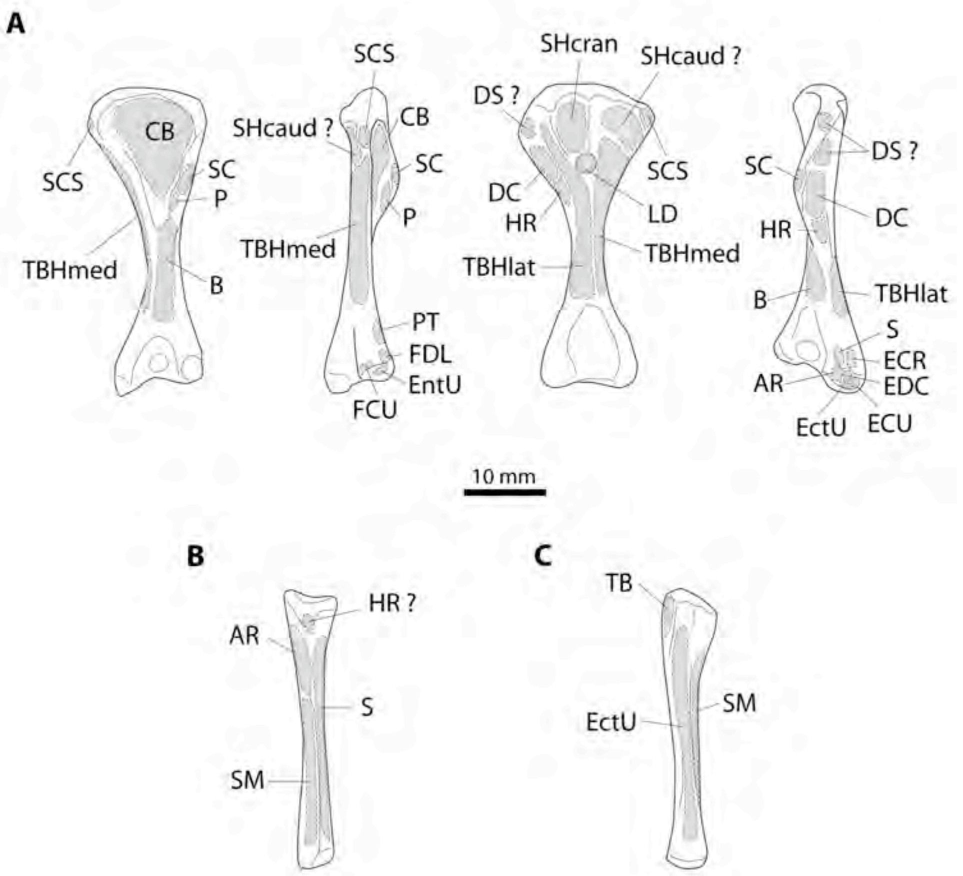

Figure 4-9. Reconstruction of muscular attachments on humerus (A), radius (B), and ulna (C) of *Euparkeria*. For explanations see text.

Lewisuchus

Muscle reconstructions for *Lewisuchus* slightly differ from those for *Euparkeria*, due to several modifications of the pectoral girdle (fig. 4-10). Most notably, the elongate scapular blade not only provides a larger area of attachment for M. deltoideus scapularis, but is also differentiated into a cranial and a caudal part (see above). The caudal part of this differentiation possibly correlates to the attachment of M. teres major, which is present in crocodilians and some ratites, and may be synapomorphic for Archosauria (chapter 3). Therefore, it is assumed here that M. teres major existed in *Lewisuchus,* too.

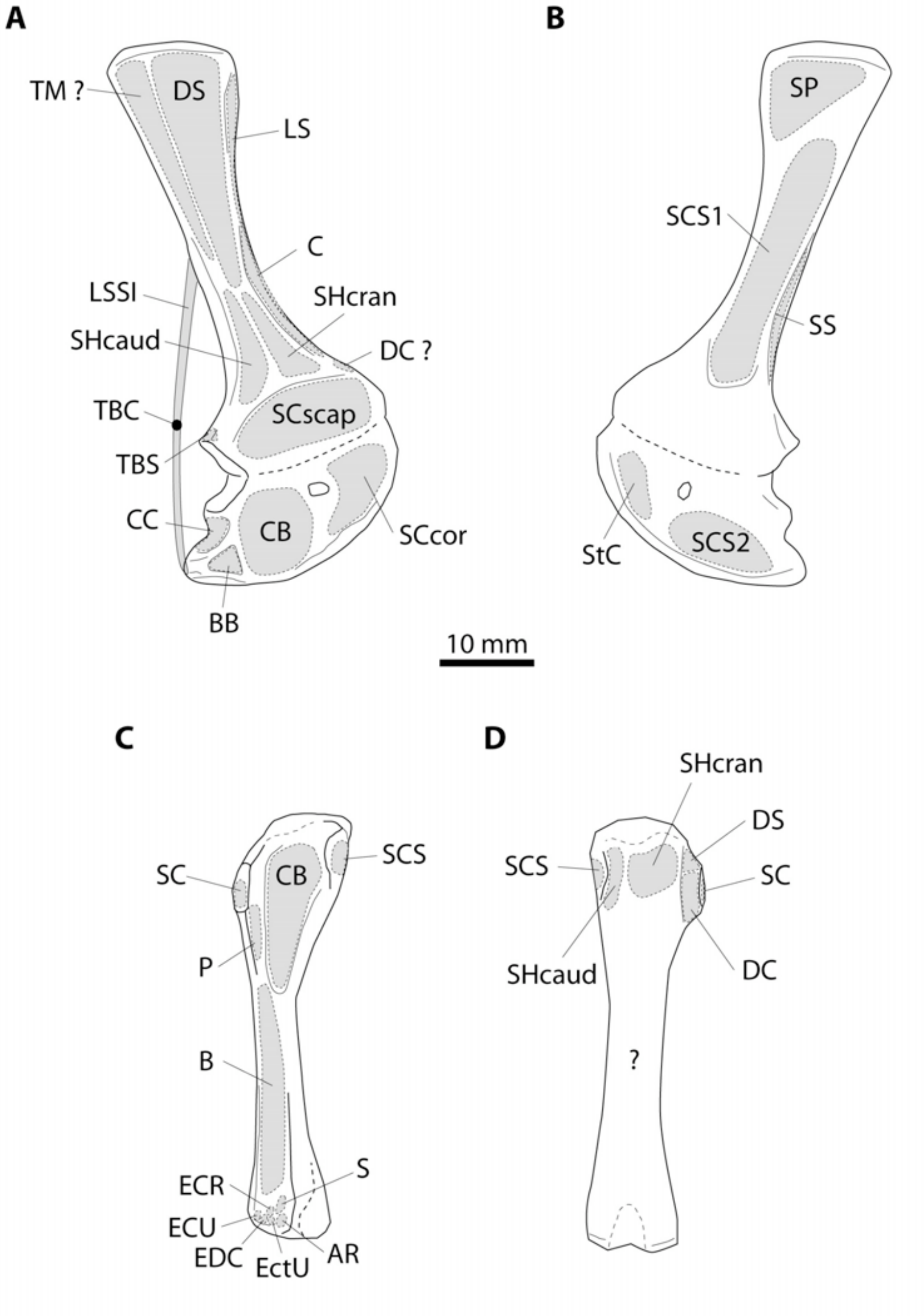

Figure 4-10. Reconstructions of the muscular attachments on the scapulocoracoid (A, lateral view; B, medial view) and humerus (C, ventral view; D, dorsal view) of *Lewisuchus*. The question mark in D indicates that dorsal surface of the humerus cannot be observed in the holotype. For explanations see text.

On the medial side of the scapular blade, the fossa for the scapular part of M. subcoracoscapularis is elongate, and extends towards the distal part of the blade. In addition, the elongate facet on the proximal caudal border probably served for the attachment of M. serratus superficialis, and represents a new osteological correlate of this muscle that is easy to recognize in many dinosaurs. Caudolateral to this facet, the minute flange that protrudes over the caudal edge of the scapular blade probably correlates to the attachment of a Ligamentum sternoscapulare internum (like in crocodilians, chapter 3), and therefore possibly indicates a crocodilian-like morphology of M. triceps brachii caput coracoscapulare (fig. 4-10). However, in birds a similar flange is correlated with M. serratus superficialis pars cranialis only.

As a consequence of the reconstruction of M. triceps brachii caput coracoscapulare proposed here, the caudoventromedial tubercle of the coracoid possibly served for the ventral attachment of the Ligamentum sternoscapulare internum. The distinct comma-shaped subglenoid fossa probably correlates to the insertion of M. costocoracoideus, as in *Euparkeria*. The large, triangular tubercle cranioventral to this structure is identified as the origin of M. biceps brachii. The remaining muscles that arise from the coracoid, M. supracoracoideus and M. coracobrachialis, cannot be delimited unambiguously. There is no indication that a cranial extension of M. pectoralis might have attached to the coracoid.

On the observable parts of the humerus, the pattern of muscle attachments resembles *Euparkeria*. Differences result from deviant proportions of the bone, i.e. the more elongate diaphysis and the less expanded proximal and distal ends. The poor preservation and incomplete preparation of the dorsal side of the humerus renders any reconstruction of the extents of Mm. scapulohumerales speculative. Moreover, these obstacles impede the reconstruction of the humeral heads of M. triceps brachii, and prevent the localization of the scar that indicates the insertion of M. latissimus dorsi and M. teres major. A dorsocranial ridge that would correlate to the origin M. humeroradialis cannot be observed either.

Discussion

Based on skeletal restorations (figs. 4-2, 4-5) and reconstructed muscular attachments (figs. 4-8, 4-9, 4-10), lines of action of several muscles of the forelimbs of *Euparkeria* and *Lewisuchus* can be inferred. The cingulo-axial muscles exhibit no major changes from basal archosaurs to dinosauriforms. The form of the cranial edge of the scapular blade is consistent with a plesiomorphic, ventral insertion of M. cucullaris (figs. 4-11, 4-13). Furthermore, phylogenetic inference suggests that a M. rhomboideus was present in the last common ancestor of birds and crocodilians that probably inserted on the medial side of the suprascapular cartilage (chapter 3). The rugose dorsal edge of the scapula in both *Euparkeria* and *Lewisuchus* probably indicates the presence of such a suprascapular cartilage. Since

M. serratus profundus seems to have shifted its insertion onto the dorsal part of the medial scapula, the suprascapula might have served solely for the attachment of M. rhomboideus. Following this argumentation, M. rhomboideus possibly was present in *Euparkeria* already (figs. 4-12, 4-14). Due to the elongate neck of dinosauriforms, the cranial extent of M. serratus profundus probably was reduced relative to neck length, in order to maintain effective lines of action (fig. 4-12, 4-14). The same might be true for M. levator scapulae, but considering the orientations of neck and scapula, the muscle would have maintained an effective course even if it preserved its plesiomorphic extent (fig. 4-11, 4-13).

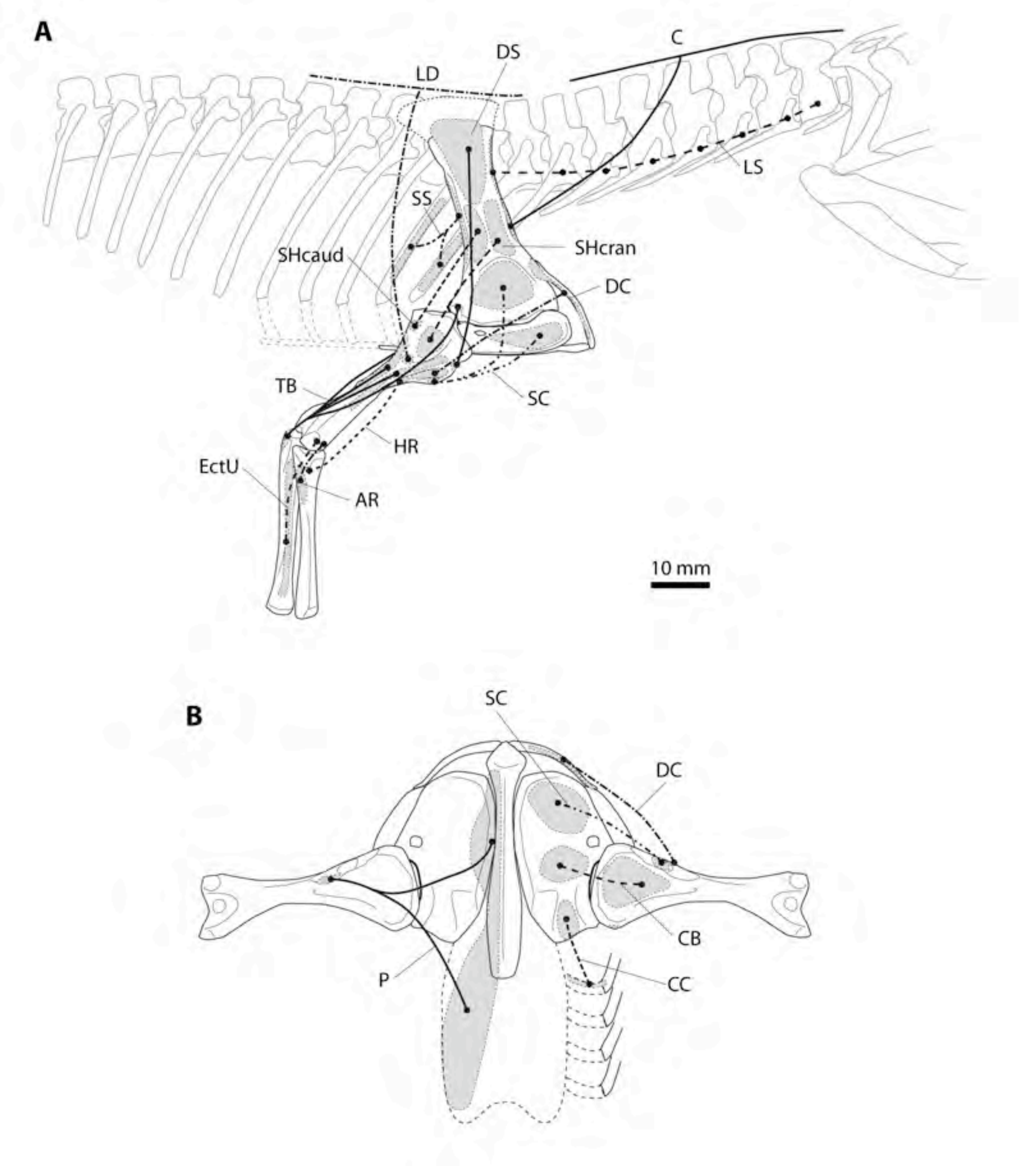

Figure 4-11. Reconstruction of the skeletomuscular system of the pectoral girdle and forelimb of *Euparkeria*, superficial part. A, lateral view; B, ventral view. Muscles are depicted by their estimated lines of action, giving a gross idea of the function of each muscle.

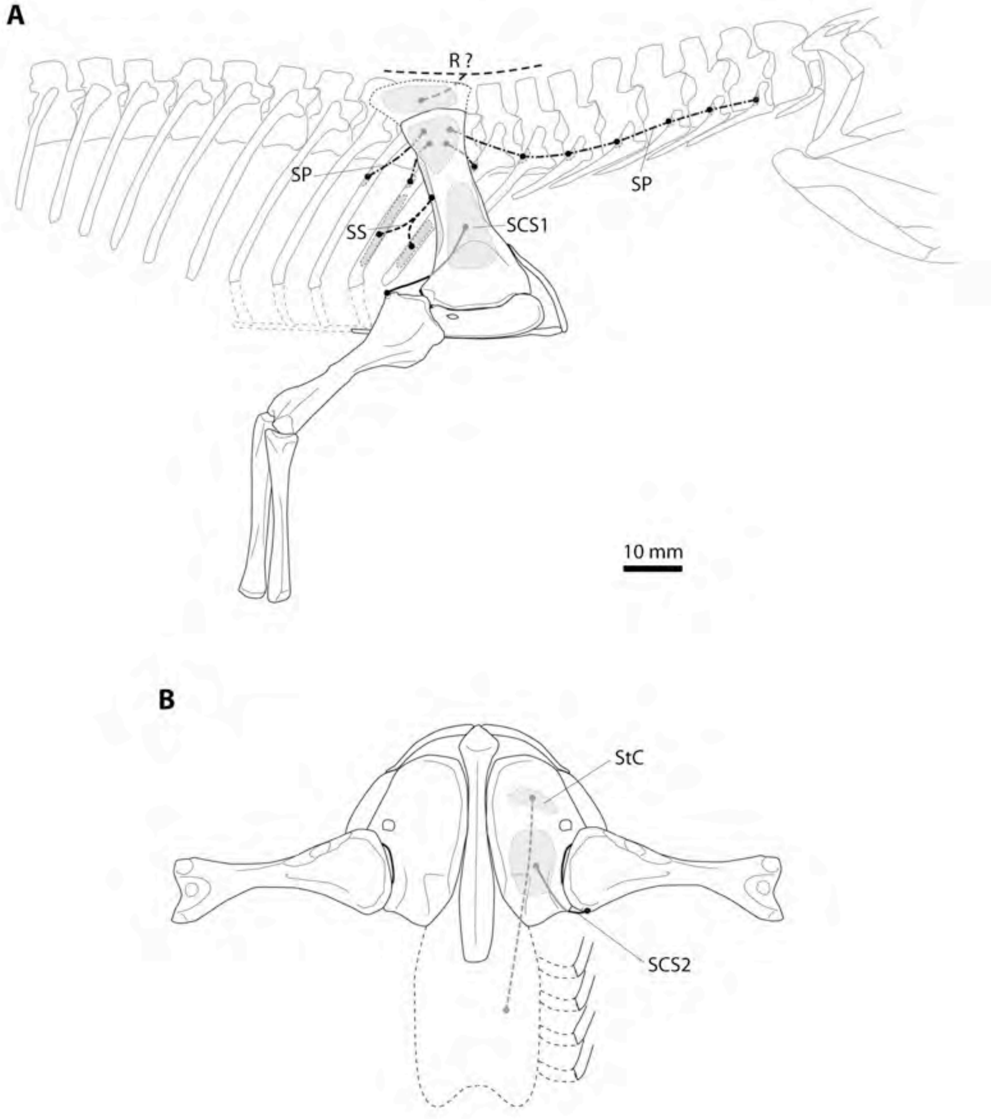

Figure 4-12. Reconstruction of the skeletomuscular system of the pectoral girdle and forelimb of *Euparkeria*, deep part. A, lateral view; B, ventral view. Muscles are depicted by their estimated lines of action, giving a gross idea of the function of each muscle. Shaded attachment areas and lines of action indicate muscles that lie on the remote side of the respective bone.

No differentiation of the caudal edge of the scapular blade can be observed in *Euparkeria*, but basal dinosauriforms seemingly restricted the insertion of M. serratus superficialis to the medial side of the blade (fig. 4-14). Moreover, a crocodilian-like configuration of M. triceps brachii caput coracoscapulare appears realistic (fig. 4-13). The possible presence of M. teres major in *Lewisuchus* (fig. 4-13) represents a derived feature that also resembles crocodilians. These inferences support earlier observations that *Euparkeria* had not yet acquired all characters of the Archosauria (Sereno, 1991; Juul, 1994; Parrish, 1997; Gower and Weber, 1998; Benton, 2004): a similar pattern is also reflected in muscular anatomy.

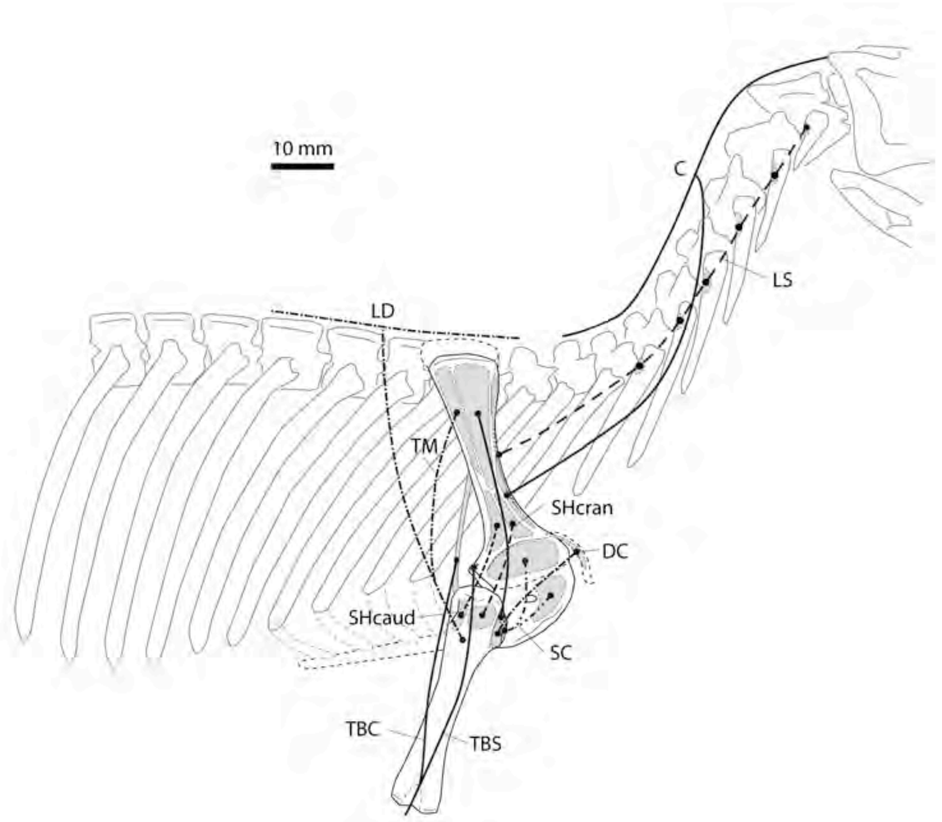

Figure 4-13. Reconstruction of the skeletomuscular system of the pectoral girdle and forelimb of *Lewisuchus*, superficial part. Muscles are depicted by their estimated lines of action, giving a gross idea of the function of each muscle.

In *Euparkeria*, the pectoral girdle is almost as wide as high, rendering the cross-section of the animal circular in this part of the body (fig. 4-2). In contrast, *Lewisuchus* has a scapular blade that is dorsally elongate, arguing for a dorsoventrally high and transversely slender profile of the cranial trunk (fig. 4-5). Furthermore, the coracoid of *Euparkeria* has a horizontal orientation and forms the major portion of the glenoid. This configuration allows for an optimal transfer of forces with a major medial and a minor vertical component, indicating a sprawling posture of the humerus. In *Lewisuchus*, the scapular part of the glenoid is enlarged relative both to the scapular head and to the coracoidal part. Given its caudolateral orientation, the glenoid is therefore optimized to transfer dorsomedially directed forces.

The reconstructed lines of action of the main protractor and retractor muscles (M. deltoideus clavicularis, M. supracoracoideus, M. pectoralis) are oriented in a subhorizontal plane in *Euparkeria* (fig. 4-11). The accurate angle of orientation of the coracoid in *Lewisuchus* is hard to determine since the scapulocoracoid is diagenetically compressed, but it appears to have faced more ventrolaterally than ventrally. Thus, in comparison with *Euparkeria* the line of action of M. supracoracoideus has a stronger vertical component (fig. 4-13). The same might be true for M. deltoideus clavicularis, but the course of this muscle is speculative since no clavicles are preserved.

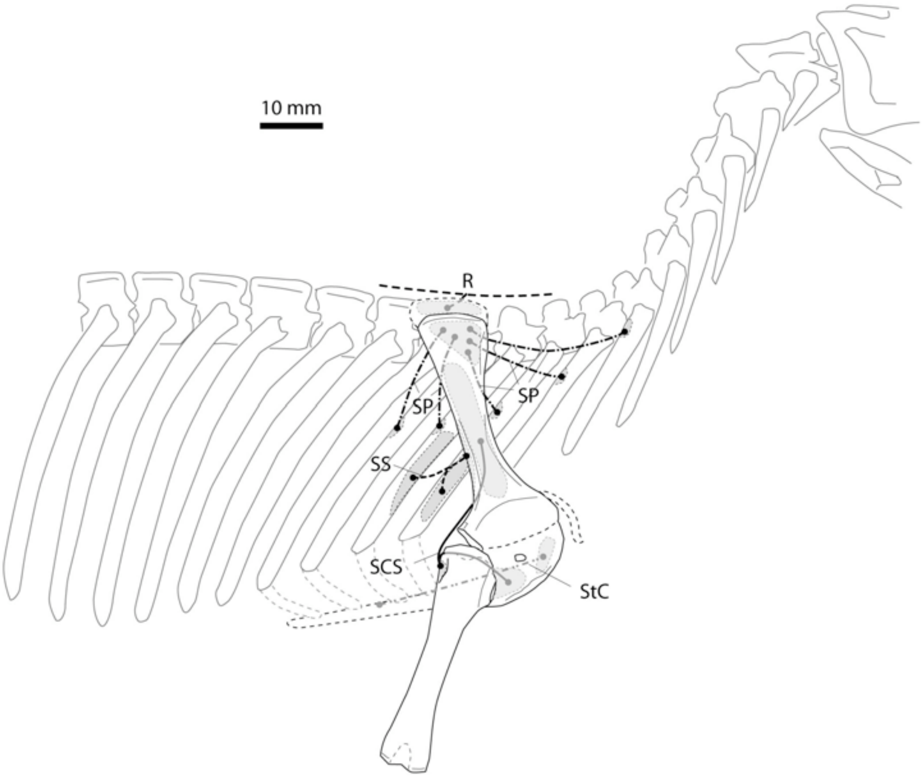

Figure 4-14. Reconstruction of the skeletomuscular system of the pectoral girdle and forelimb of *Lewisuchus*, deep part. Muscles are depicted by their estimated lines of action, giving a gross idea of the function of each muscle. Shaded attachment areas and lines of action indicate muscles that lie on the remote side of the respective bone.

The areas of origin and insertion of M. coracobrachialis are relatively large in *Euparkeria*. It is to note that the area of a fleshy attachment is primarily controlled by the angle of insertion, not necessarily by the volume of the corresponding muscle (Bryant and Seymour, 1990; chapter 3). Anyway, the size of the osteological correlates of M. coracobrachialis supports a rather sprawling posture of the humerus. The large scar for the insertion of its antagonist, M. latissimus dorsi, substantiates this interpretation (fig. 4-11). This system might have been somewhat weaker in *Lewisuchus*, but the data are to incomplete to draw definite conclusions. As far as it can be inferred, the configuration of the M. triceps brachii system seems to be conservative in *Euparkeria.* In *Lewisuchus*, the origins of M. triceps brachii caput scapulare and caput coracoscapulare have shifted dorsally (fig. 4-11, 4-13). Possibly, this reconfiguration is correlated with a more ventrolateral orientation of the humerus.

Finally, the hemispherical shape of the distal condyles of the humerus, their wide spacing, and the simple, concave form of the proximal articular facets of radius and ulna will have allowed for considerable rotation in the elbow joint of *Euparkeria*. If the insertion of M. humeroradialis is correctly identified, this muscle might have assisted in axial rotation of the radius, and in pronation of the manus (fig. 4-11). Other muscles that have their origin or insertion on the forearm (M. abductor radialis, M. ectepicondylo-ulnaris, M. supinator manus) show a crocodilian-like configuration (fig. 4-11), obviously indicating shared derived traits of archosauromorphs.

Considering general proportions, the size of the humerus of *Lewisuchus* (relative to the size of the scapulocoracoid and to total body size) is not significantly different from *Euparkeria* (table 4-1). The relation of forelimb to hind limb length is hard to estimate in *Lewisuchus*, since radius, ulna, and femur are missing (Romer [1972b] mentions a femur and a tibia, but the specimen actually preserves a tibia and a fibula). Moreover, the length of the dorsal vertebral column is hard to estimate in *Lewisuchus*, since the preserved vertebral column ends with dorsal vertebra 8. Therefore, the sole morphometric relation that can be calculated and compared to *Euparkeria* is that of humerus to tibia length: this value is 0.79 in *Euparkeria* and 0.43 in *Lewisuchus*.

Taxon	**SL**	**HL**	**RL**	**FL**	**TL**	**DVL**	**SL/HL**	**HL/TL**
Euparkeria (SAM 5867)	38	38	32	56	48	140*	1.0	0.79
Lewisuchus (PVLR 01)	44	46	-	-	106	-	0.96	0.43

Table 4-1. Comparison of simple morphometric measurements of forelimbs and hindlimbs in *Euparkeria* and *Lewisuchus*. *The dorsal vertebral length is an estimate based on individual vertebrae of SAM 5867 and the complete vertebral column of SAM 6047. Abbreviations: **SL**, scapula length; **HL**, humerus length; **RL**, radius length; **FL**, femur length; **TL**, tibia length; **DVL**, length of dorsal vertebral column.

Conclusions

Regarding bone morphology and muscle system, *Euparkeria* exhibits a mosaic of plesiomorphic features and advanced characters. As Ewer (1965) already pointed out, no adaptation to bipedality can be recognized in the forelimb. The strong development of the horizontally oriented protractors and retractors, as indicated by the considerable size of the deltopectoral crest, and the form and orientation of the glenoid indicate a sprawling to semi-erect position of the humerus during locomotion. This view is also supported by the significant development of the M. coracobrachialis – M. latissimus dorsi system, and the morphology of the elbow joint, which allows for considerable rotation.

In *Lewisuchus*, the dorsoventrally deep body alone is indicative of increased cursoriality, and made a relative elongation of the scapular blade necessary. According to glenoid shape and coracoid orientation, the humerus had a more semi-erect, less sprawling posture. The development of a crocodilian-type M. triceps brachii caput coracoscapulare might be related to this change. However, there are no strong indications for bipedality in the forelimb. The elements that are essential for evaluating the type of locomotion (radius, ulna, manus) are not preserved. The humerus to tibia ratio indicates a significant difference between *Lewisuchus* and *Euparkeria* (table 4-1), which may be interpreted as an adaptation to cursoriality and at least facultative bipedality (Coombs, 1978a). However, trunk and forelimb of *Lewisuchus* are incompletely preserved, precluding a reliable assessment of significant morphometric ratios. *Lewisuchus* exhibits adaptations to an erect posture and cursorial locomotion in the hind limb (Fechner, pers. comm. 2007), but it cannot be ruled out that this taxon maintained the ability of quadrupedal locomotion. Considering the lack of forelimb material, the inference of trends towards bipedality in other Ladinian dinosauriforms (Sereno and Arcucci, 1994; Arcucci, 1997; Sereno, 1997; Carrano, 2000) is speculative.

In summary, the available data about the early evolution of the forelimb on the line to dinosaurs is rather incomplete and leaves room for speculation. Since distal elements (radius, ulna, manus) are missing, no conclusions can be drawn about the origin of bipedality. Good cranial material is also wanting, rendering the ecology of these early dinosauriforms enigmatic until more complete specimens are found. At least with respect to forelimb evolution, the rise of the dinosaurs lies more in the dark than previously thought.

5 Structure and function of the forelimb in basal saurischians and early theropods

Introduction

Our understanding of the rise of the Dinosauria is still hampered by an incomplete fossil record, low numbers of well-preserved specimens, and ambiguous phylogenetic relationships. The first known dinosaurs were found in Middle Carnian sediments of Argentina (Reig, 1963; Casamiquela, 1967; Sereno et al., 1993) and Brazil (Colbert, 1970; Bonaparte et al., 1999, 2007; Langer et al., 1999). Many of these early forms are incomplete, but current data suggest that at that time, dinosaurs already had differentiated into the main subgroups Ornithischia, Sauropodomorpha, and Theropoda (Novas, 1996; Sereno, 1997; fig. 5-1).

Already with the late 19th century dinosaur discoveries, it became evident that these animals evolved various types of locomotion. Some groups were recognized as habitual bipeds (theropods, some ornithopods; e.g., Wagner, 1861; Leidy, 1865; Cope, 1867; Huxley, 1869), others as graviportal quadrupeds with fully erect limbs (sauropods; e.g., Hulke, 1874; Osborn and Granger, 1901; Osborn, 1904), and some were reconstructed as quadrupeds with sprawling forelimbs (stegosaurs, ceratopsians; e.g., Marsh, 1891; Lull, 1905, 1910). The question about the ancestral type of dinosaurian locomotion arose only lately, following the application of cladistic methodology to fossil archosaurs and the recognition of dinosaurs as a monophyletic group (Bakker and Galton, 1974; Benton, 1984, 1990; Gauthier, 1984, 1986). Sereno (1991, 1997) suggested that ornithodirans acquired a fully erect gait first, then changed to bipedality and finally evolved the ability to flight, first in pterosaurus and some 50 million years later in birds. This model implies that all ornithodirans, including basal ornithischians and sauropodomorphs, are plesiomorphically bipedal, and developed secondary quadrupedalism independently in several lineages (Stegosauria, Ankylosauria, Ceratopsia, some ‘prosauropods’, and Sauropoda). However, these arguments have been weakened by evidence for obligate quadrupedal pterosaurs (Mazin et al., 1995; Unwin, 1996, 1999). Moreover, recent studies show that basal dinosauromorphs like *Lagerpeton* had no fully erect hind limb (Fechner, in prep.), and that the data is ambiguous regarding the type of locomotion of basal dinosauriforms like *Lewisuchus* (chapter 4; Fechner, in prep.). Based on the ichnological record of dinosaurs and their early relatives, Thulborn (2006) even argued that Dinosauria is a polyphyletic assemblage, because the foot postures and types of locomotion observable in the earliest ornithischian and sauropodomorph tracks resemble the plesiomorphic (basal archosaurian) type, and lack the strong adaptations for bipedality and erect stance that are seen in theropods. Clearly, all theropods are obligate bipeds, and the same is true for herrerasaurids. In a similar manner, Sereno et al. (1993) reconstructed one of the earliest dinosaurs known, *Eoraptor lunensis*, as a biped with grasping hands, but no detailed anatomical study of this critical taxon has been published. A closer look at the osteology of basal saurischians like *Eoraptor* and *Herrerasaurus*, a comparison to basal theropods and ornithischians, and a reconstruction of the forelimb musculature of these forms may give better ideas about the early evolution of locomotion in dinosaurs. Which transformations of the forelimb occurred in parallel to the improvements of the hind limb? Are the same transformations visible in all lineages of early dinosaurs, or do different lineages exhibit different trends? And do the forelimbs of *all* early dinosaurs show adaptations related to habitual bipedality? These questions will be addressed in this chapter.

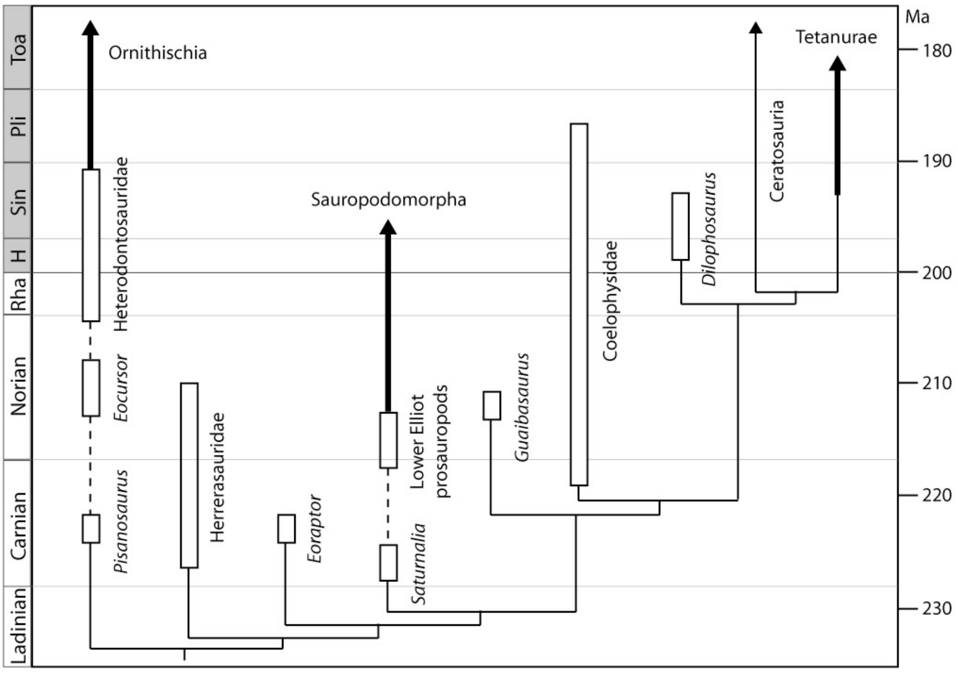

Figure 5-1. Relationships and temporal distribution of the early dinosaurs discussed in this chapter (Sauropodomorpha, which will be addressed in the following chapters, are also shown). Cladogramm based on Rauhut (2003a) and Langer and Benton (2006).

Anatomy

Note: The neutral orientation of the humerus relative to the body in early dinosaurs is not entirely clear and will be addressed later in this chapter. Therefore, in the following descriptions developmental orientations are used (see chapter 2).

Basal saurischians

The early saurischians *Eoraptor* and *Herrerasaurus* are key taxa for our understanding of the forelimb evolution of early dinosaurs, since both are relatively well preserved and comprise complete hand skeletons. Especially *Eoraptor* is of interest, because this genus lacks many of the specializations seen in *Herrerasaurus* and may exhibit a forelimb *bauplan* that is close to that of the ancestral dinosaur.

Eoraptor

Scapulocoracoid. The shoulder girdle of *Eoraptor lunensis* (PVSJ 512; figs. 5-2, 5-3, 5-4) closely resembles that of the basal dinosauriforms *Lewisuchus admixtus* and MCZ 9483 (‘*Lagosuchus talampayensis*’). Like in these forms, the scapular blade is elongate and has a straight, transversely thickened and rounded caudal edge and a concave, transversely narrow and sharp cranial border. The distal expansion is moderate, but in *Eoraptor* the blade is less slender than in *Lewisuchus*. The distal half of the lateral side of the blade is flattened, except the caudolaterally deflected caudodorsal border. The proximal half of the blade is smoothly rounded towards the caudal edge and somewhat flattened in the center. There is no indication of a flange on the caudal border. Since the medial side of the scapular blade cannot be observed, there is no clue regarding the presence of a caudomedial facet for M. serratus superficialis (see chapter 4).

Dorsal to the glenoid, a large, oval, rugose scar faces caudodorsolaterally. Proximocranially, there is a wide, triangular depression, extending dorsocranially from the middle of the base of the blade. Like in *Lewisuchus*, the scapular head is wide craniocaudally and narrow dorsoventrally. A large, oval fossa extends over most of its lateral surface. This fossa has differentiated into a deep depression in its cranial two thirds, and a shallow caudal part. Craniodorsally, the acromial region bears an elongate, spindle-shaped, dorsolaterally oriented facet. Ventrolateral to this facet, the acromial ridge extends caudally for about one third of the length of the caput, and forms the craniodorsal border of the aforementioned fossa. The sutural line has a distinct step in the caudal part of its course, the caudal-most part of the suture being more ventrally placed than the remaining part (fig. 5-2). The scapular portion of the glenoid has a subquadrangular outline, and bears a faint glenoid lip dorsolaterally. Cranially, a triangular recess connects the glenoid cavity to the lateral fossa on the scapular head. A strong, bulging glenoid lip borders the coracoidal portion of the glenoid laterally and caudally. The articular facet of the coracoidal glenoid portion is lozenge-shaped and slightly concave.

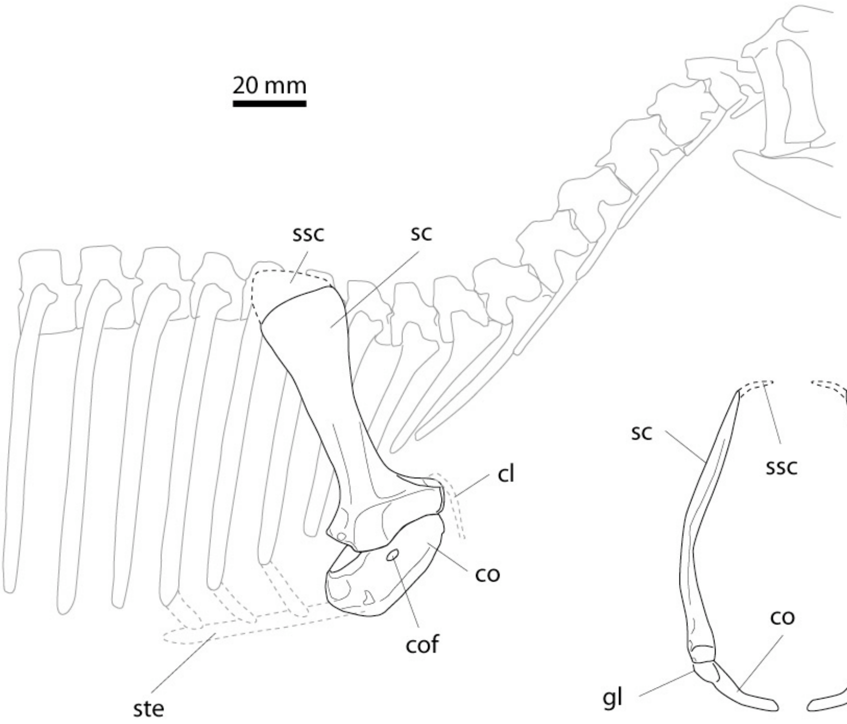

Figure 5-2. Reconstruction of the shoulder girdle of *Eoraptor lunensis*, based on PVSJ 512. Center, lateral view; right, caudal view. The cranial and axial skeletal elements are schematically drawn.

The coracoid is characterized by a strongly developed craniocaudal ridge, which divides the element into a dorsolateral and a ventromedial half (figs. 5-2, 5-3). In cranial view, both sections enclose an angle of about 130°. The coracoid foramen is relatively large. It is situated directly cranioventral to the caudal kink in the sutural line. Craniodorsally on the lateral face of the coracoid, there is a triangular depression. The shallow, subrectangular subglenoid fossa is bordered by narrow ridges laterally and caudally, and by a wide shelf medially. The ventromedial corner of the coracoid bears a relatively small, triangular biceps tubercle. Moreover, *Eoraptor* exhibits a smoothly rounded caudomedial process on the coracoid that is somewhat larger than the biceps tubercle. The medial edge of the coracoid is thickened and rounded, but narrows cranially. As for the scapula, the medial side of the coracoid cannot be examined.

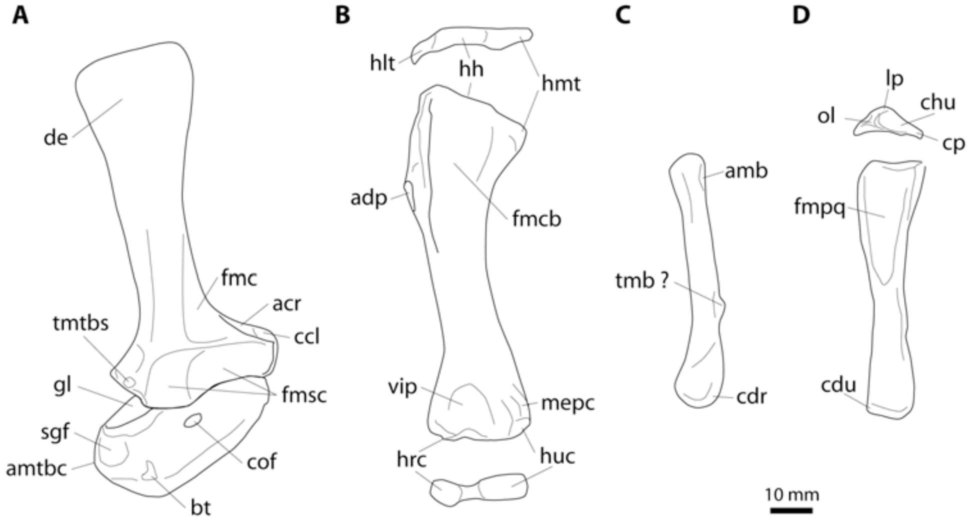

Figure 5-3. Osteological structures of the forelimb elements of *Eoraptor lunensis* (PVSJ 512). A, scapula in lateral view. B, humerus in proximal, ventral, and distal views. C, radius in lateral view. D, ulna in proximal and medial views.

Humerus. Like in *Lewisuchus*, the humerus of *Eoraptor* has about the same length as the scapula. It is moderately elongate and has a robust, transversely wide shaft (fig. 5-3). The proximal and distal ends are expanded. The distal end is twisted with an angle of about 40° relative to the transverse axis of the proximal expansion. The subrectangular humeral head is slightly concave ventrally and extends onto the shaft dorsally. The lateral tuberosity is dorsoventrally deep, convexly rounded, and somewhat dorsally deflected with respect to the base of the humeral head. The proximal base of the medial tuberosity is enlarged and slightly ventrodistally deflected. Caudally, the medial tuberosity has the form of an elongate, pointed process, and is oriented in parallel with the axis of the humeral head.

Beginning at the cranioproximal corner of the humerus, the deltopectoral crest extends for more than 50% of total humeral length. The crest is ventrally directed and relatively large. Its spindle-shaped apex projects cranially over its base and is situated in the proximodistal center of the crest. The distal half of the apex exhibits a ventrocaudally-deflected facet. The caudal side of the deltopectoral crest is slightly concave proximally, and flat distally. The straight ventral edge of the distal part of the crest tapers off with a low angle relative to the shaft axis. Proximally, the ventral side of the humerus is flat and bears no distinct fossa. The same is true for the ventral side of the shaft. The caudal side of the shaft is wide and convex. Ventrodistally, the intercondylar depression is triangular and widely separates the ulnar and radial condyles. The subrectangular ulnar condyle is wider craniocaudally than deep dorsoventrally. The entepicondyle exhibits a lancet-shaped facet, which is bordered by a ridge cranially. The distal part of this facet exhibits a rugose, oval depression. The caudoventral corner of the ulnar condyle bears a large tubercle. The radial condyle is oval and deflected about 20° ventrally relative to the transverse axis of the ulnar condyle.

Antebrachium. The radii and ulnae of *Eoraptor* are compressed and deformed, especially on the left body side, and do not show many details (fig. 5-3). The radius slightly curves distocaudally, rendering its cranial edge convex and the caudal edge concave. The proximal end is enlarged and bears a cup-shaped cotyle for articulation with the humerus. Craniomedially on the proximal end, there is a 2 mm long, proximodistally oriented crest. Where uncompressed, the shaft has a subcircular cross-section. An intermuscular ridge is visible on the proximal half of the medial side of the right radius, and forms the cranial margin of an elongate facet on the caudomedial shaft. In the distal third of the medial shaft, another intermuscular ridge runs obliquely from the cranial edge to a large tubercle caudally. Craniodistal to this tubercle, there is a spindle-shaped facet. Distally on the craniolateral side of the shaft, an unusually prominent, three-sided tubercle projects craniolaterally and is bordered by an elongate depression medially. The distal end of the radius is expanded and curved in transverse direction, rendering the cranial side of the distal antebrachium convex and the caudal side concave. Due to compression, the natural orientation of the transverse axis of the distal end of the radius cannot be reliably assessed. The medial side of the distal end is somewhat flattened, and a small tubercle projects from its craniomedial corner. The caudomedial corner of the distal radius is in close contact with the ulna, probably showing the natural articulation of the two elements.

The proximal end of the ulna bears a relatively long cranial process that has a bulging edge. The humeral cotyle is strongly concave craniocaudally but only slightly concave transversely. The triangular lateral process is placed in the caudal third of the proximal expansion. Caudoproximally, the olecranon process has the form of a low, rounded prominence, but there is no proximally projecting ossification. In proximal view, the medial border of the articular head is concave. A small process projects caudomedially from the caudal corner of the proximal ulna. On the medial side of the shaft cranial to this process, there is large triangular fossa that extends distally for about half the length of the shaft. The shaft is transversely narrow and curved, with a convex lateral side and a concave medial side. In caudal view, the ulnar shaft exhibits a round swelling immediately distal to its proximal third. A similar swelling is found on the cranial edge of the shaft, proximal to the distal third of the shaft.

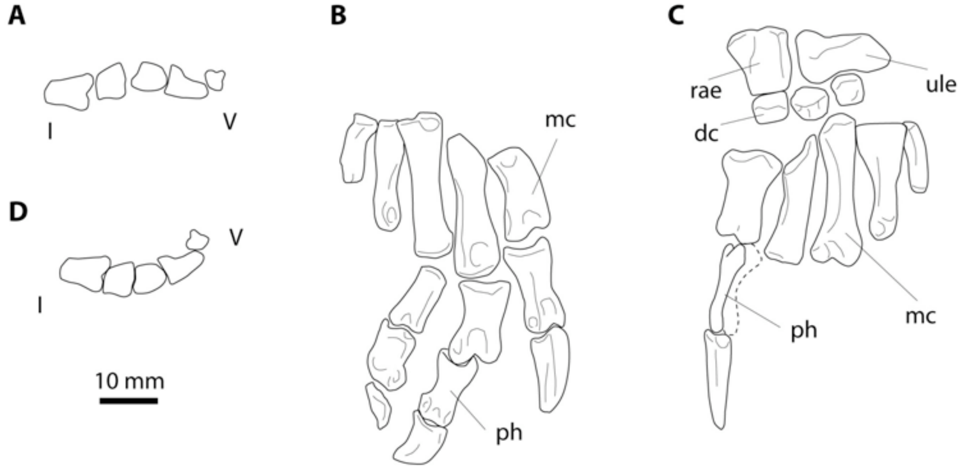

Figure 5-4. Hand skeleton of *Eoraptor,* as preserved in PVSJ 512. A, proximal view; B, dorsal view; C, ventral view. D, reconstruction of the original articulation of the metacarpals in proximal view.

Manus. Both manus were found articulated (fig. 5-4), albeit the left one is strongly deformed. All metacarpals are fully developed, without any strong reduction of the lateral two metacarpals. These are somewhat shorter and less robust than metacarpals I–III, but not significantly more so than e.g. in crocodilians (see figs. 3-18, 5-5).

Carpus. Carpal elements are observable only on the ventral side of the left manus. These include radiale, ulnare, and three distal carpals articulating with metacarpal II, III, and IV, respectively. Distal carpals that articulate with the peripheral metacarpals may be present on the dorsal side of the specimen, but cannot be observed because this side is not fully prepared. There is no indication for the presence of a centrale.

The radiale is large and somewhat elongate proximodistally, possibly due to diagenetic deformation. The proximomedial corner of its ventral side exhibits a small subquadrangular facet. In proximal view, the ulnare is oval and concave. From its ventromedial corner, a small process projects ventrally. The ventral side of the ulnare is transversely wide but proximodistally short. It bears a small oval depression medially, possible for articulation with a pisiforme. In distal view, the ulnare has a convex articular facet that is in contact with the third distal carpal.

Distolaterally, the radiale articulates with a subrectangular distal carpal that in turn has contact to another distal carpal laterally, and to metacarpal I distally (fig.

5-4). Presumably, this element represents distal carpal I. The ventral side of distal carpal I bears a lateral and a medial tubercle. The second distal carpal is wedge-shaped, with a tapering ventral side, and is situated close to metacarpals II and III. The proximal and distal sides of this element are flat and rectangular in outline. A small tubercle protrudes from its ventrolateral corner. The third distal carpal has a cubic shape with rounded edges and corners, and articulates with the ulnare proximally and metacarpals III and IV distally. A small tubercle projects from its proximomedial corner. The distal face of the element is convexly rounded.

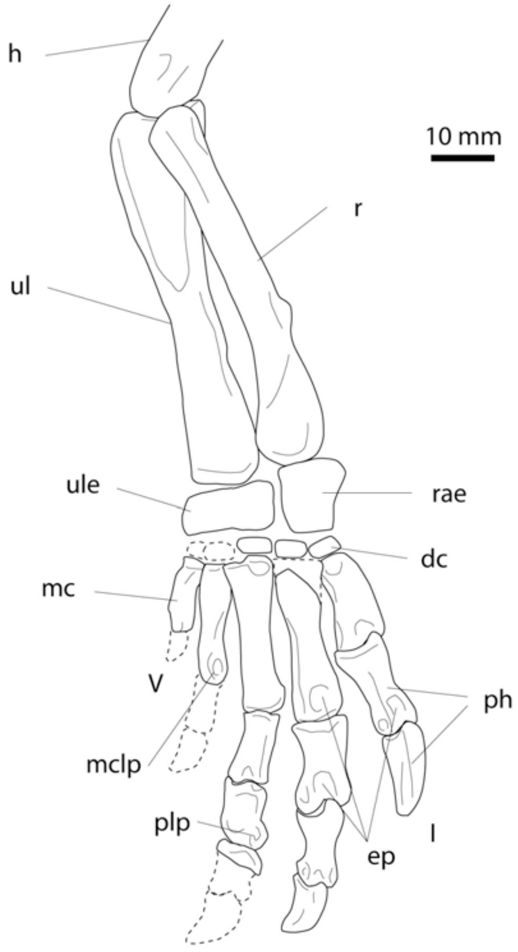

Figure 5-5. Reconstruction of the right arm of *Eoraptor* in dorsocranial view. Note the prominent ligament pit distomedially on metacarpal IV.

Metacarpus. Metacarpal I has the largest ratio of midshaft diameter to total length, and is therefore the most robust of all metacarpals (figs. 5-4, 5-5). The proximal end has a trapezoid shape and is convex transversely. A prominent, three-sided tubercle projects from its ventrolateral corner. The dorsal side of the shaft is craniomedially oriented, and has a smoothly rounded medial margin. Dorsolaterally, a prominent flange extends along the proximal third of the bone. The dorsal side of the proximal shaft exhibits a deep, oval depression. The shaft of metacarpal I slightly curves distolaterally. Proximally on the dorsal side of the distal end, there is a faint depression. The proximolateral face of the shaft exhibits a triangular depression that tapers distally. The ventral side of the shaft is wide and flattened. Proximally, an oblique ridge runs from the proximomedial corner to the lateral side, ending after about one third of the length of the bone. The distal condyles of metacarpal I are strongly asymmetric. The lateral condyle extends far more distally, and is about twice as large as the medial condyle. Both condyles are separated by a narrow groove. In distal view, the medial condyle is oval, with a dorsoventrally oriented long axis. A tubercle is situated on the ventromedial corner of the medial condyle. The ligament pits on both sides of the distal end are shallow and have no distinct margins.

The proximal end of metacarpal II has a transversely narrow, parallelogram-shaped outline (fig. 5-4). The medial part of the proximal end and the proximal articular surface are not preserved. Dorsolaterally, a wide, rounded flange extends distally for about one quarter of the total length of the bone. The shaft of metacarpal II has a suboval cross-section, with the wider side facing dorsomedially. The dorsal side of the shaft is transversely convex, its ventral side flat. On the distal third of the dorsal shaft, there is an oval facet that is clearly offset from the proximal part of the shaft. A small, shallow depression is situated centrally on this facet. The form of the distal condyles cannot be observed.

Metacarpal III is subequal in length to metacarpal II (fig. 5-5). Its proximal expansion is twice as wide as that of metacarpal II. The articular surface is dorsoventrally convex and has a trapezoid shape, with the longest edge on the ventral side. The dorsomedial corner is distally deflected and projects dorsally; the ventromedial corner is enlarged, rounded, and also distally deflected. On the medial face of the ventromedial corner, there is a slightly concave facet for articulation with metacarpal II. The lateral edge of the proximal end is also concave, and serves for articulation with metacarpal IV. Dorsolaterally, there is no distinct flange like in metacarpals I and II. The dorsal side of the shaft is flattened, while the ventral side is transversely convex. Distally, metacarpal III is expanded and bears a facet on its dorsal side, similar to that of metacarpal II. The distolateral side of metacarpal III exhibits a large, circular ligament pit that is bordered by narrow ridges. The distal articular end is subdivided into two symmetrical condyles that are visible in ventral view.

Metacarpal IV is significantly more slender than the preceding metacarpals (fig. 5-5). Its planar proximal end has a subtriangular, transversely elongate form. Ventroproximally, metacarpal IV widely overlaps metacarpal III. The slender shaft has a circular cross-section and a shallow depression proximally. The distal expansion is subtriangular with a tapering ventral side. It is strongly laterally rotated: the axis through the ligament pits is oriented almost perpendicular to the dorsal edge of the proximal expansion. The medial ligament pit is very deep, but the lateral ligament pit is only weakly developed. The distal condyle is convex in all directions.

The relatively small, peg-like metacarpal V is slender and has a subrectangular proximal end. The shaft is oval in cross-section. Distally, there is a rounded, conical process. No other details are observable.

Digits. Phalanges are fully preserved in digiti I-III only. The form of the distal end of metacarpal IV and the presence of ligament grooves implies that phalanges originally were developed in digit IV (fig. 5-5), but lost prior to fossilization or during preparation. In the left hand, a rudimentary phalanx is preserved in articulation with metacarpal V, but the distal end of this element is broken off. Therefore, the phalangeal formula for *Eoraptor* can only be stated as 2-3-4-(≥1)-(≥1). Other basal dinosaurs such as *Heterodontosaurus* (fig. 5-12; Santa Luca, 1980) and basal sauropodomorphs (chapters 6 to 8) count 2-3-4-3-2 (see also Galton and Upchurch, 2004; Norman et al., 2004; Butler et al., 2007a).

The robust first phalanx of digit I exhibits a subtriangular, asymmetrical proximal articular facet, which (unlike other dinosaurs) has no central ridge that subdivides the facet in a lateral and a medial cotyle. The dorsal side of the shaft is concave proximodistally, but planar transversely. Laterally, the shaft is rounded; the ventral side is flat. Distally, a circular pit deeply excavates the dorsal base of the articular end. Distolaterally and distomedially to this pit, small tubercles project distally. The lateral and medial sides of the distal expansion bear large, deep ligament pits that are bordered by wide, rounded ridges. The ungual of digit I is not enlarged relative to the remaining unguals, but exhibits a slight asymmetry (its lateral side is steeper and flattened). The first ungual is not strongly curved; only the distal tip is slightly ventrally deflected. On the ventral side of the ungual, an elongate flexor tubercle extends over the entire proximal half of the claw. Nutritive sulci are present only in the distal half of the ungual.

The first phalanx of the second digit is even more robustly developed and also slightly asymmetric, with the lateral part of the distal condyle extending further distally. The dorsoproximal edge exhibits a large, semilunate extensor tubercle.

An elongate flange protrudes from the proximal part of the dorsomedial edge. As for phalanx I.1, a deep circular pit characterizes the dorsal side of the distal end. Both the lateral and the medial sides of the distal expansion exhibit ligament pits, but the medial pit is only weakly developed. Phalanx II.2 is more slender than II.1, has no clear extensor process proximally and lost the medial ligament pit. Instead of a circular depression, the dorsal side of the distal end exhibits a trapezoid facet. The ungual of digit II is strongly developed and wider than that of digit I, but shows no strong curvature either. On both sides of the claw, deep sulci are present that follow its curvature distally, but have a sigmoid course proximally.

The proximal phalanx of digit III is significantly shorter than phalanx II.1. Because all sides of the shaft are planar, the element appears block-like. Proximally, there is a transversely wide, oval extensor tubercle. Like the other proximal phalanges, the dorsal side of the distal end bears a circular pit. The distal articular condyles are separated by a deep groove, and appear to be symmetric. The remaining phalanges are strongly damaged, impeding any observation of details. Phalanges III.2 and III.3 are both shorter than the preceding phalanx. The ungual of digit III has a shape similar to the unguals of digits I and II.

Herrerasaurus

The anatomy of the pectoral girdle and forelimb of *Herrerasaurus* has already been described in detail by Sereno (1993). Novas (1993) used some of the characters described by Sereno (1993) for a revised diagnosis of *Herrerasaurus*. Diagnostic characters include a proximally projecting medial tuberosity that is separated from the humeral head by a deep channel, a ridge-like entepicondyle that is bordered by depressions dorsally and ventrally, and an elongate manus that reaches 60% of the combined lengths of humerus and radius (Novas, 1993). Moreover, Sereno (1993) regarded following additional characters as autapomorphic for *Herrerasaurus*: a saddle-shaped ulnar condyle; a concave-convex, sliding articulation between ulna and ulnare; a centrale that is placed distal to the radiale; and an enlarged distal carpal IV that articulates with metacarpals IV and V.

Furthermore, the anatomy of the hand of *Herrerasaurus* lead Novas (1993) to emend the diagnosis of Saurischia, adding two characters: first, the proximal bases of metacarpals IV and V overlap the preceding metacarpal on its palmar side; second, the first phalanx of the first digit is longer than metacarpal I. Novas (1993) interpreted other characters as synapomorphic for *Herrerasaurus* + Theropoda, including a humerus that reaches only 50% of femoral length, deep extensor pits distally on metacarpals I–III, strongly reduced metacarpals IV and V, elongate penultimate phalanges, and enlarged, strongly curved unguals on digits II and III that bear prominent flexor tubercles.

In order to avoid redundancies, the following description lists only additional observations of forelimb characters, especially those relevant for muscle reconstructions.

Note: Sereno (1993) uses the term ‘acromion’ in a sense synonymous with the terms ‘scapular head’ or ‘caput scapulae’ of this work. Following the terminology of Romer (1956), the term ‘acromion’ should refer only to a distinct process or facet cranially on the scapula that serves for articulation with the clavicles.

Scapulocoracoid. Sereno (1993) underscored the unusal, strap-like form of the scapular blade, which is totally unlike those of any other early dinosaur or basal dinosauriform (fig. 5-6). Adding to the description by Sereno (1993), further observations are noted in the following.

Both the cranial and caudal margins of the scapular blade are sharply tapering. The proximocranial part of the lateral face of the blade exhibits an elongate facet in PVSJ 605, but not in PVSJ 53. A low flange slightly protrudes from the caudal border of the blade, distal to its proximal third. Medially to this flange, an elongate, sickle-shaped facet extends over the proximal two-thirds of the blade. The proximal part of this facet extends cranially to the midst of the blade. The acromial region of the caput bears a rugose, suboval tubercle that faces craniodorsolaterally. The apical end of the clavicle (which is not known in *Herrerasaurus*) probably articulated with this facet. The lateral side of the scapular head bears an elongate fossa that extends only over its cranial two thirds. There is no distinct acromial crest. Immediately dorsal to the glenoid, a triangular, rugose scar faces caudolaterally. The medial side of the scapular head exhibits a subtriangular depression craniodorsally and a moderate swelling (the preglenoidal buttress) caudally. The sutural line between scapula and coracoid has a characteristical caudal kink. The coracoidal part of the glenoid connects to the lateral side of the coracoid via a distinct furrow, which is located somewhat ventral to the suture. Ventral to the glenoid, the subglenoid fossa has a semilunate shape and exceeds the coracoidal part of the glenoid in size. The subglenoid fossa is bordered craniolaterally by a rounded ridge. This ridge bears a small tubercle at mid-length. The coracoid foramen is small and caudally placed, about 12 mm distant from the sutural line.

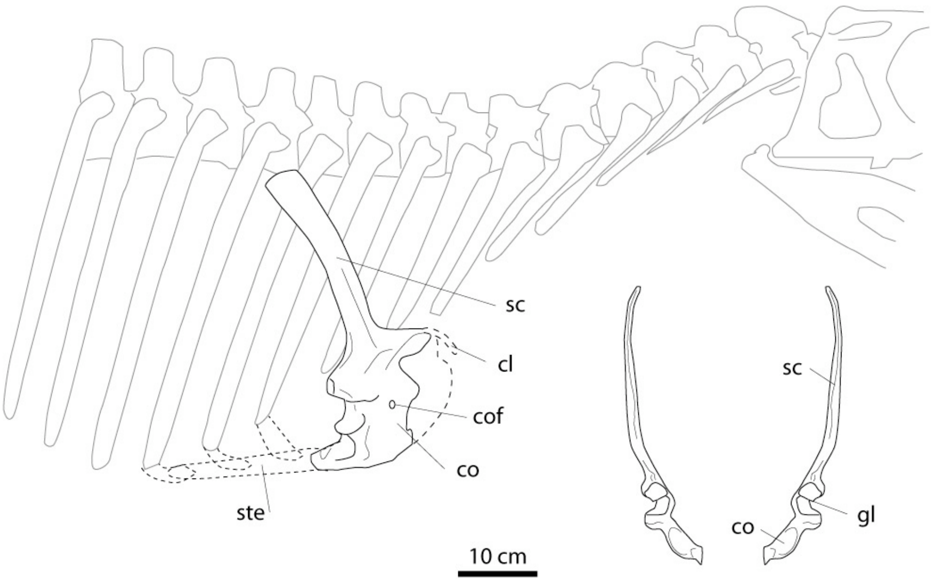

Figure 5-6. Reconstruction of the shoulder girdle of *Herrerasaurus ischigualastensis*, based on PVSJ 605. Center, lateral view; right, caudal view. The cranial and axial skeletal elements are schematically drawn.

Humerus. The humerus (fig. 5-7) is characterized by a large, rectangular deltopectoral crest that extends distally for about 40% of the length of the humerus. Novas (1993) and Sereno (1993) described the diagnostic form of the medial tuberosity, which is separated from the humeral head by deep channel. However, this channel is not present in all specimens (e.g., not in MLP 61-VIII-2-3, '*Ischisaurus*'). On the proximal edge of the humerus, ventrally to the medial tuberosity, there is a suboval, craniomedially-oriented facet. A subtriangular facet is found distally to the medial tuberosity on the dorsal side of the humerus. The humeral head slightly protrudes over the dorsal face of the shaft. In proximal view, it has a ventrally concave, kidney-like shape (Sereno, 1993). A longitudinal swelling distal to the humeral head divides the proximal part of the dorsal side of the humerus into two facets. Cranially, the lateral tubercle of the humerus is slightly thickened and bears a subcircular depression. In some specimens, the lateral tubercle is separated from the humeral head by a distinct constriction (e.g., MLP 61-VIII-2-3). A distinct ridge dorsally borders the cranial side of the deltopectoral crest. This ridge extends somewhat distally beyond the distal base of the deltopectoral crest. The distal part of the caudal side of the deltopectoral crest exhibits conspicuous striations for muscle attachment.

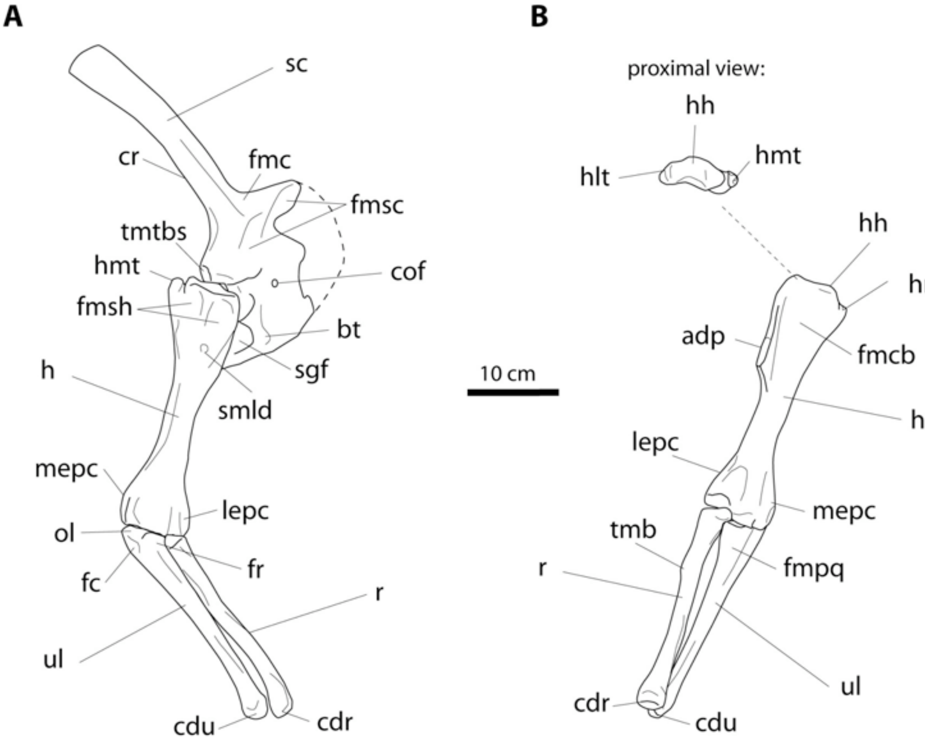

Figure 5-7. Osteological structures of the forelimb elements of *Herrerasaurus*, based on PVSJ 373. A, lateral view. B, ventromedial and proximal views.

As described by Sereno (1993), the distal end of the humerus has no clear intercondylar pits, neither ventrally nor dorsally. However, triangular depressions are present in MACN 18060. Craniomedially on the distal end, there is a distomedially-oriented facet that exhibits a circular depression. This facet is dorsally bordered by is a distinct, oval tubercle.

Antebrachium. Sereno (1993) described the distal parts of the forelimb (figs. 5-8, 5-9) in high detail, leaving not much to add. Like in *Eoraptor*, the proximal end of the radius lacks a distinct caudal process. The shaft of the radius is circular in cross-section, and exhibits a small round tubercle on the lateral side of the proximal end. Craniomedially on the proximal part of the shaft, there is a sickle-shaped facet. Another oval facet is found proximally on the lateral side of the shaft. Caudal to this facet, striations indicate a muscle attachment site. On the caudal border of the distal end, an elongate, laterally sharply bordered, peg-like tubercle serves for articulation with the ulna. Four small facets at the distal lateral edge of the radius probably indicate ligament attachment. A large tubercle is situated on the cranial edge of the distal end of the radius, and a second, smaller tubercle is found in the cranial half of the medial side of the distal expansion.

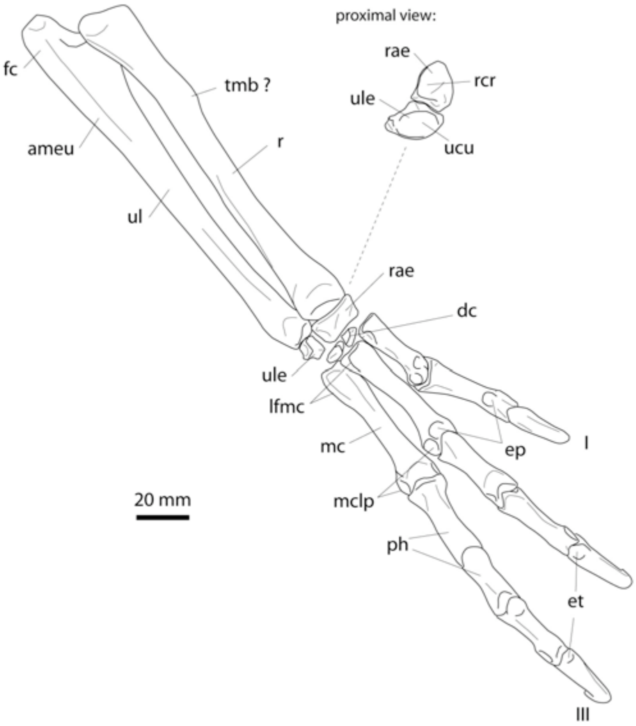

Figure 5-8. Reconstruction of the forearm and hand of *Herrerasaurus* in dorsolateral and proximal views, based on PVSJ 373 (mirrored).

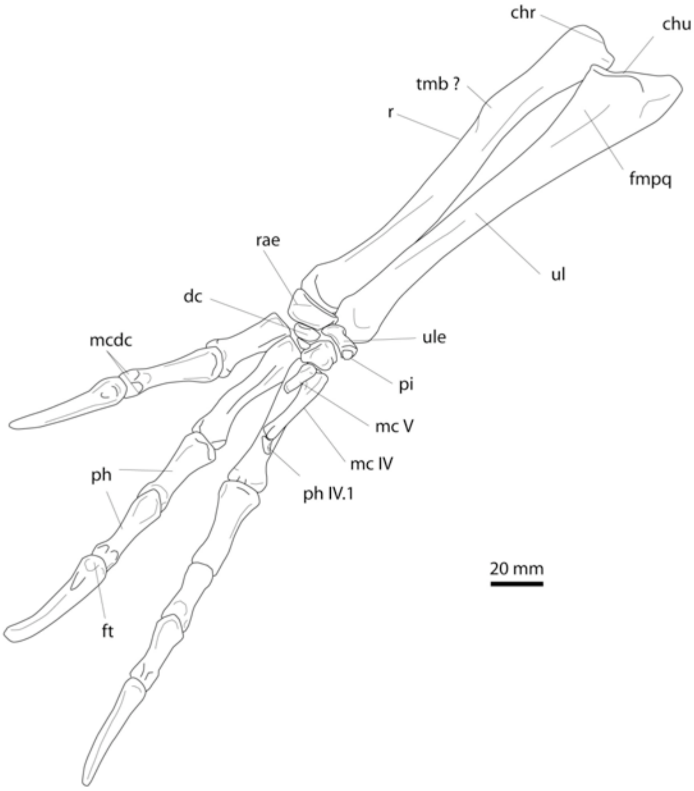

Figure 5-9. Reconstruction of the forearm and hand of *Herrerasaurus* in ventromedial view, based on PVSJ 373 (mirrored).

The proximal end of the ulna has a sigmoid medial edge. The well-developed olecranon process is not directly proximally, but caudoproximally oriented. A small triangular facet is found on the craniomedial corner of the proximal expansion. The lateral process is short, stout and pyramidal in outline. Below this process, a short ridge runs distally and slightly cranially. An oval, laterally oriented facet is caudodistally adjacent to the lateral process. While the medial side of the shaft is considerably flattened, the caudal side of the shaft is transversely convex and exhibits strong, proximodistally oriented striations. Craniomedially, a wide, concave furrow probably served for articulation with the peg-like process of the radius. An elongate, oval tubercle is found close to the distal expansion on the caudomedial edge of the shaft. Small, rugose circular facets are found medially and caudolaterally on the edge of the distal expansion.

Manus. In the hand skeleton (figs. 5-8, 5-9), the radiale exhibits a smooth, triangular facet on the distolateral corner of its dorsal side. A similar facet is found on the proximomedial corner of its ventral side. The ventral side of the ulnare has a large, hemispherical process that articulates in a corresponding socket on the radiale. Both the medial and lateral tips of the ventral ulnare bear tubercles. No additional observations could be made on the centrale and distal carpals. The proximomedial corner of the ventral side of metacarpal I exhibits a rugose, triangular facet. A circular depression is found on the proximal dorsal side of this metacarpal. The proximal dorsolateral edges of metacarpals I, II, and III are extended to flanges that slightly overlap the succeeding metacarpal. On the proximolateral corner of metacarpal IV, there is an elongate, ovoid tubercle. The distal ends of these metacarpals have differently formed ligament pits laterally and medially, the lateral ones being larger. Sereno (1993) mentioned the strong asymmetry of the distal end of metacarpal I, which is also medially rotated relative to the proximal expansion. In metacarpals II and III, the medial and lateral sides of the distal expansion are somewhat dorsally rotated. The ventral side of the distal expansion of metacarpal I is characterized by a wide, transversely concave depression. The proximal phalanx of digit I exhibits a triangular facet proximally on its ventral face. The extensor tubercle proximally on the ungual of digit I is only weakly developed. As in *Eoraptor*, the nutritive sulci are restricted to the distal part of this ungual. Ventrally, the flexor tubercle has a faint, transversely oriented incision on its proximal face. The tubercle is separated from the proximal articular surface of the ungual by a weak constriction.

Basal theropods

Although not in focus of this thesis, a consideration of the forelimb anatomy of basal theropods will help to better understand the beginnings of saurischian forelimb evolution, and to recognize specializations within Sauropodomorpha. Therefore, a short summary of anatomical changes from basal dinosaurs to basal theropods, coelophysoids, and ceratosaurs will follow. For a general review of basal theropod anatomy, see Rowe and Gauthier (1990) and Tykoski and Rowe (2004).

More or less complete forelimbs are known from the basal-most theropod known, *Guaibasaurus candelariensis*, the coelophysoids *Dilophosaurus, Coelophysis*, *Segisaurus*, and *Liliensternus*, and the basal ceratosaur *Ceratosaurus* (Marsh, 1892; Gilmore, 1920; von Huene, 1934; Rühle von Lilienstern et al., 1952; Welles, 1984; Colbert, 1989; Rowe, 1989; Bonaparte et al., 1999; Carrano et al., 2005; Bonaparte et al., 2007). *Coelophysis* is accepted here to include '*Syntarsus' rhodesiensis* and *'S.' kayentakatae*, following Downs (2000) and Bristowe and Raath (2004). Regarding the general *bauplan* of the pectoral girdle and forelimb, all these forms have in common a straight, sometimes elongate (Carrano et al., 2005) scapular blade with a marked distal expansion (contrasting the more straplike scapula of higher theropods), and a rather straight humerus (in contrast to the strongly sigmoidal shape of later forms).

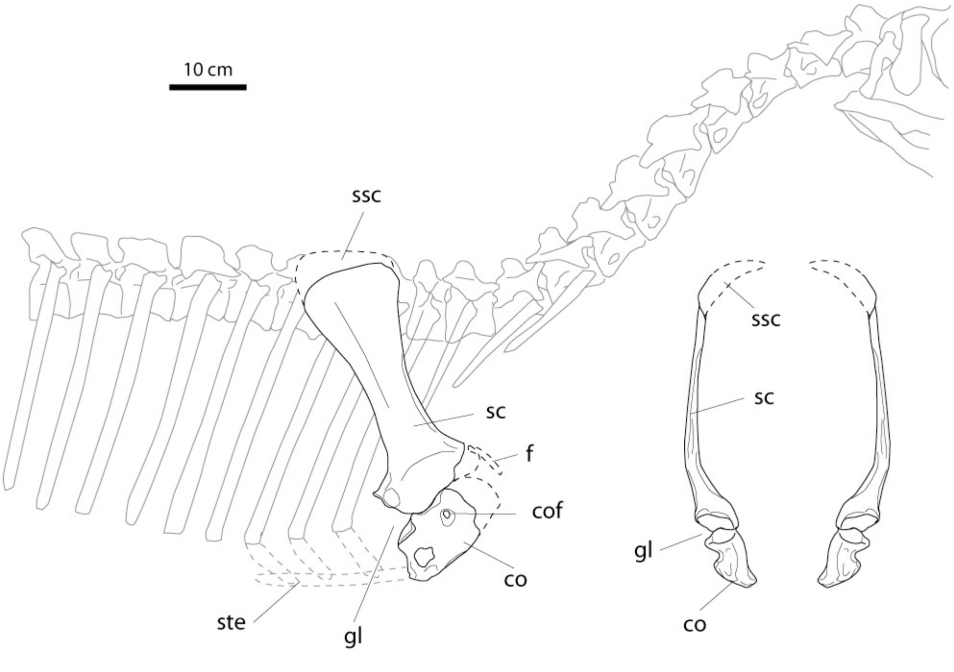

Figure 5-10. Reconstruction of the shoulder girdle of *Dilophosaurus wetherili*, based on UCMP 37302. Left, lateral view; right, caudal view. The cranial and axial skeletal elements are schematically drawn.

Scapulocoracoid. Major modifications with respect to forms like *Lewisuchus* and *Eoraptor* include: a larger distal expansion of the scapula (Tykoski and Rowe, 2004) that extends caudally beyond the caudal border of the blade; a clear differentiation of the proximal scapular blade into a larger cranial and a smaller caudal facet; the development of a distinct acromial ridge dorsal to the ventrolateral fossa on the scapular head (only in *Dilophosaurus* and higher theropods, fig. 5-10); and a more cranioventral position of the biceps tubercle on the coracoid. The unusual, rectangular shape of the scapular blade of *Dilophosaurus*, which is depicted in Welles (1984), and often cited as an autapomorphy of this taxon (e.g., Rauhut, 2003a; Tykoski and Rowe, 2004), is actually an artefact. Personal observation led to the recognition of a fault that runs obliquely through the left scapula, and displaces its distal end cranioproximally. In contrast, the right scapula has a form comparable to that of other basal theropods (fig. 5-10). A small flange on the proximal part of the caudal side of the blade, medially accompanied by a sickle-shaped facet, is present in all basal forms. The ventrolateral fossa on the scapular head is restricted to the cranial part of the bone in *Liliensternus* and *Dilophosaurus.* In *Dilophosaurus* and higher theropods, the subglenoid fossa is not caudally, but caudolaterally to laterally oriented, and less clearly delimited than in more basal dinosaurs (Welles, 1984).

Furculae. Furculae are known from *Coelophysis* and *Segisaurus* (Raath, 1977; Tykoski et al., 2002; Rauhut, 2003a; Carrano et al., 2005; Rinehart et al., 2007). In both genera, each clavicle has a slightly sigmoidal form and thickens ventrally where the right and left elements fuse. The proximal end is somewhat flattened and articulates with the acromion facet of the scapula (Carrano et al., 2005; Rinehart et al., 2007). In *Segisaurus* and *Coelophysis kayentakatae*, a distinct, striated epicleidal facet is preserved (Tykoski et al., 2002; Carrano et al., 2005).

Humerus. The humerus of *Guaibasaurus* is characterized by its relatively long deltopectoral crest that extends for the entire proximal half of the bone, resembling the condition found in *Eoraptor* and basal sauropodomorphs (Bonaparte et al., 2007; see chapter 6). Other basal theropods usually have the following derived characters in common: the humeral head has a parallelogram-like shape in proximal view; it projects above the developmentally ventral side of the shaft; the medial tuberosity is inclined caudodorsally relative to the main axis of the proximal expansion of the humerus; like in *Eoraptor*, the apex of the deltopectoral crest has a cranial projection beyond the cranial face of the crest; the apex is oriented in parallel to the shaft axis; the proximodorsal side of the humerus is flattened; and the dorsal intercondylar groove is reduced, as in *Herrerasaurus*. Other characters show no clear trend, e.g., the form of the proximolateral process, the relative length of the deltopectoral crest and the form of its distal base. The humerus of *Dilophosaurus* exhibits a number of characters not visible in other coelophysoids, including a distal end that is ventrodistally deflected, forming an angle of about 20° with the axis of the shaft. Moreover, the distal end is ventrocranially rotated for about 60°, relative to the main axis of the proximal expansion. In *Dilophosaurus* and *Liliensternus,* a large, distocaudally directed, lozenge-shaped facet is found on the caudal side of the ulnar condyle. The ventral intercondylar depression is completely lost in *Dilophosaurus*.

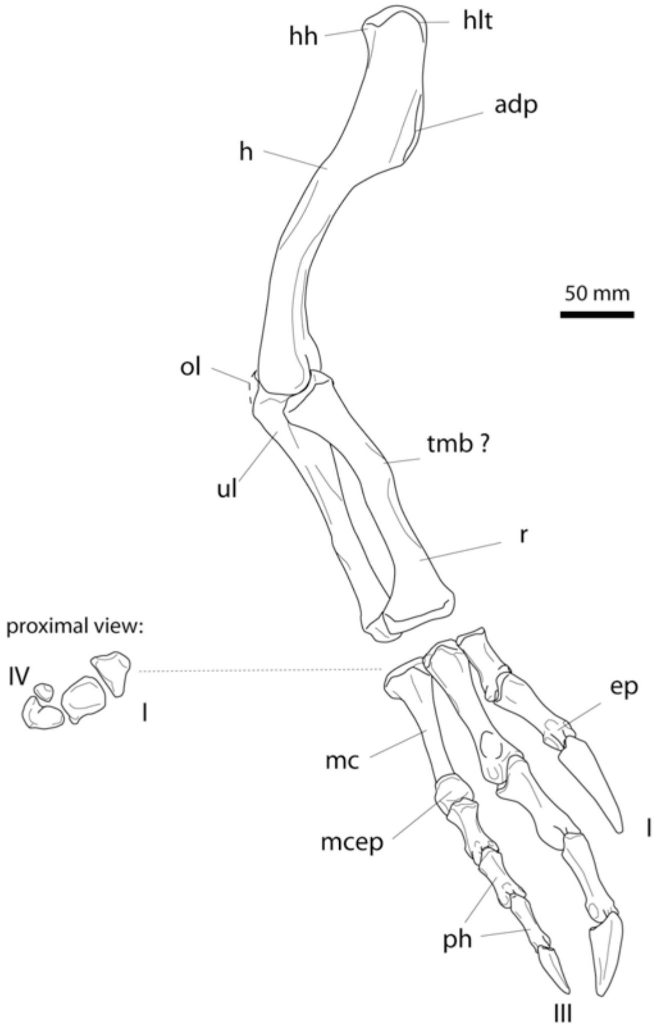

Figure 5-11. Reconstruction of the forelimb of *Dilophosaurus* in dorsolateral view, based on UCMP 37302 (mirrored). Left, metacarpus in proximal view.

Antebrachium. The forearm elements of basal theropods are relatively short and stout. In contrast to *Herrerasaurus*, the proximal and distal expansions are marked. Among basal theropods, the form of the proximal articular facet and the grade of transverse compression of the shaft of the radius is variable. A cranial tubercle ('biceps tubercle', see Discussion below) is usually present. *Coelophysis* is unique in exhibiting no tubercle for articulation with the ulna on the distal part of the shaft, and having the distal end of the radius only slightly expanded (see also Colbert, 1989). In *Dilophosaurus*, the medial edge of the distal expansion bears a projecting shelf.

An elongate cranial process characterizes the proximal end of the ulna of basal theropods. Usually, the lateral process of the proximal end is reduced in size and has a three-sided pyramidal outline. In addition, the proximal articular surface is strongly concave, and a distinct olecranon process is present. However, this latter feature could not be found in *Guaibasaurus* (Bonaparte et al., 2007). *Ceratosaurus* exhibits a deviant morphology, with a robustly rounded and caudally placed lateral process, an articular surface that is convex in its cranial part, and the absence of an ossified olecranon process (instead, there is a rugose swelling that probably formed the base for a cartilaginous expansion; see Gilmore, 1920:fig. 59). *Coelophysis* is specialized in having a prominent cranial expansion of the distal articular end.

Manus. Relatively complete hands are preserved in *Guaibasaurus*, *Coelophysis*, *Dilophosaurus*, and *Ceratosaurus* (Marsh, 1892; Gilmore, 1920; Galton, 1971b; Raath, 1977; Welles, 1984; Colbert, 1989; Bonaparte et al., 2007). Like *Herrerasaurus*, all these taxa exhibit four phalanx-bearing digits, but no vestigal metacarpal V could by identified. Usually, basal theropods have a relatively conservative carpus that preserves radiale, ulnare, intermedium (not found in *Coelophysis*), and three distal carpals capping the metacarpals (Galton, 1971b; Welles, 1984; Colbert, 1989). The first distal carpal is enlarged and overlaps the proximal ends of metacarpals I and II (Rauhut, 2003a). No carpals are ossified in *Ceratosaurus* (Gilmore, 1920). The phalangeal formula counts 2-3-4-1 in *Coelophysis* and *Dilophosaurus* (and possibly also in *Guaibasaurus*; Bonaparte et al., 2007), but is unknown for *Ceratosaurus* where only phalanges II.1, III.1, and IV.1 are preserved. Following characters are shared by all basal theropods: metacarpal I is only half as long as metacarpal II, the proximal end of metacarpal I has a trapezoid shape, the metacarpals have asymmetric distal articular condyles (the asymmetry is reduced in metacarpal III of *Dilophosaurus* and lost in the same element of *Ceratosau-*

rus), deep extensor grooves are present distally on the dorsal side of the metacarpals, the shaft of metacarpal III is significantly more slender than that of metacarpal II, accompanied by a digit III that is shorter than digit II (Rauhut, 2003a), and the unguals have a relatively low curvature. Other details of the hand anatomy vary: Metacarpal I and digit I are most robust in *Dilophosaurus*, but weaker than metacarpal II and digit II in *Coelophysis*. The first metacarpal and digit are considerably reduced in *Ceratosaurus*. The size of the ligament pits varies interspecifically and from digit to digit. *Coelophysis* exhibits elongate penultimate phalanges, but this character is only weakly developed in *Dilophosaurus*.

Basal ornithischians

Ornithischians have not been included in this study, but the early evolution of locomotion in these animals is a worthwhile question for future research. Recent phylogenetic studies suggest that heterodontosaurids are the basal-most ornithischians known (Butler et al., 2007a,b). The postcranial anatomy of *Heterodontosaurus* has been described in detail by Santa Luca (1980), and was reviewed by Weishampel and Witmer (1990) and Norman et al. (2004). Based on these works, the forelimb anatomy of this form will shortly be summarized below, in order to assess the observations in basal saurischians described above in a larger context. Implications for trends in dinosaurian forelimb evolution will be discussed in length in chapter 9.

Scapulocoracoid. The scapular blade is elongate and slightly expands distally, exhibiting a knob-like process caudally. As in other basal dinosaurs, the rugose distal end indicates the presence of a cartilaginous suprascapula. The cranial edge of the blade is slightly concave, while the caudal edge is straight over most of its length. A distinct tubercle for the origin of M. triceps brachii caput scapulare is located dorsocaudally to the glenoid on the lateral face of the scapular head. The wide glenoid is primarily caudoventrally oriented. Ventrally to the glenoid, an ovoid tubercle for the attachment of M. biceps brachii projects from the coracoid. Scapula and coracoid are firmly fused. Moreover, Santa Luca (1980) reported the presence of a sternal plate.

Humerus. The humerus of *Heterodontosaurus* is relatively robust and has an untwisted shaft, leading to parallel axes of the proximal and distal ends. The medial tuberosity is enlarged. The cranioventrally directed deltopectoral crest is large, strong and extends over 40% of the total length of the humerus. Its distal base ends abruptly, standing perpendicular to the shaft. Distocaudally, a prominent entepicondyle projects over the surface of the shaft. The ectepicondyle has the form of a ridge that proximally projects from the rim of the radial condyle. The asymmetrical distal condyles do not extend onto the dorsal side of the humerus, and a distinct intercondylar fossa is missing on this side. The ulnar condyle reaches somewhat more distally than the radial condyle. Both condyles are relatively large and considerably extend onto the developmentally ventral side of the humerus. There is no intercondylar depression on the dorsal side of the humerus, although the ulna bears a well-developed olecranon process.

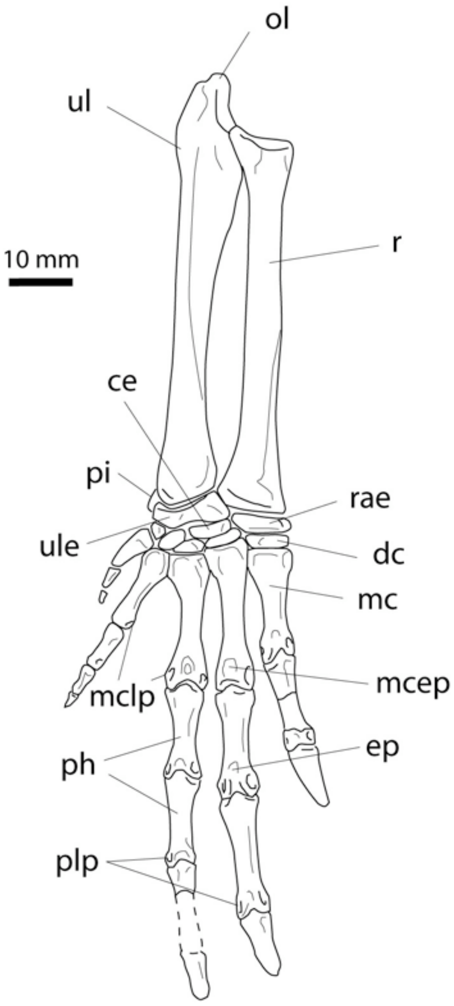

Figure 5-12. Antebrachium and manus of *Heterodontosaurus tucki* in dorsolateral view. Redrawn after Santa Luca (1980).

Antebrachium. The radius of *Heterodontosaurus* is relatively long, attaining 70% of the length of the humerus. The subcircular proximal end bears a proximomedially projecting process caudally and a tuberculous swelling laterally. Caudally on the distal end, there is a tubercle for articulation with the ulna (Weishampel and Witmer [1990] assumed this tubercle to have served for muscle attachment).

Relative to the proximal ends, the distal ends of both radius and ulna are medially rotated.

The ulna has a prominent olecranon process. The caudal face of this process is thickened and striated. A distinct intermuscular crest that runs obliquely in disto-lateral direction is found on the proximal two thirds of the lateral side of the shaft. This crest separates two attachment sites of antebrachial musculature (see below).

Manus. *Heterodontosaurus* has an especially plesiomorphic carpus that comprises nine elements, including ulnare (probably fused with the intermedium), radiale, pisiform, centrale, and distal carpals I–V (fig. 5-12). The pisiform articulates with the distal end of the ulna and the ulnare. The hand is relatively large, surpassing radius and ulna in length and reaching almost the length of the humerus. The proximal articular surfaces of metacarpals I and II are extended onto the dorsal surface of the shaft, indicating the possibility of strong extension of the manus. Metacarpal I is asymmetric, with a twisted and more distally projecting lateral distal condyle. The distal ends of metacarpals I–III bear deep extensor pits. As in other basal dinosaurs, digits IV and V are reduced in size. The phalangeal formula of *Heterodontosaurus* counts 2-3-4-3-2. The phalangeal joints of digits I–III are asymmetric, causing medial deviation during extension and lateral deviation during flexion. The unguals are large and bear prominent flexor tubercles, unlike those of other ornithischians.

Muscle reconstructions

Based on phylogenetic inference made possible by a study of extant reptilian forelimb musculature (chapter 3), and by comparison to *Euparkeria* and *Lewisuchus* (chapter 4), muscle attachment sites are reconstructed here for *Eoraptor*, *Herrerasaurus*, and *Dilophosaurus*. Among basal theropods, the latter taxon is best preserved, and its anatomy is regarded here as representative for basal theropods with unreduced arms and hands. The general configuration of the forelimb musculature in these forms is similar to that of basal dinosauriforms, but there are some important differences. However, due to imperfect preservation (especially in *Eoraptor*), some inferences have to remain ambiguous.

Scapulocoracoid (fig. 5-13). In *Eoraptor*, the caudal part of the scapular blade exhibits no facet for M. teres major. Cranioproximally on the blade, the large triangular depression seems to be homologous with the sickle-shaped facet for M. cucullaris of basal dinosauriforms. Hence, the area of insertion of this muscle is relatively enlarged in *Eoraptor*. However, this narrows down the room for the origins of Mm. scapulohumerales, implying a more proximodistal than craniocaudal configuration of these muscles. A second possibility is a shift of the origin of M. scapulohumeralis caudalis towards the caudal edge of the blade. The poor state of preservation of the base of the scapular blade does not allow for definite conclusions here. The differentiation of the ventrolateral fossa on the scapular head into two distinct areas is a new character that may reflect a separation of M. supracoracoideus pars scapularis into two individual heads. The remaining muscle attachments resemble *Lewisuchus*, however with a relatively small and more cranially placed tubercle for the origin of M. biceps brachii on the coracoid, and a more laterally placed tubercle for the origin of M. triceps brachii caput scapulare on the scapula. Since no caudal flange on the scapular blade could be recognized, no Ligamentum sternoscapulare internum is reconstructed. However, given the phylogenetic position of *Eoraptor*, this ligament probably was also present in this form.

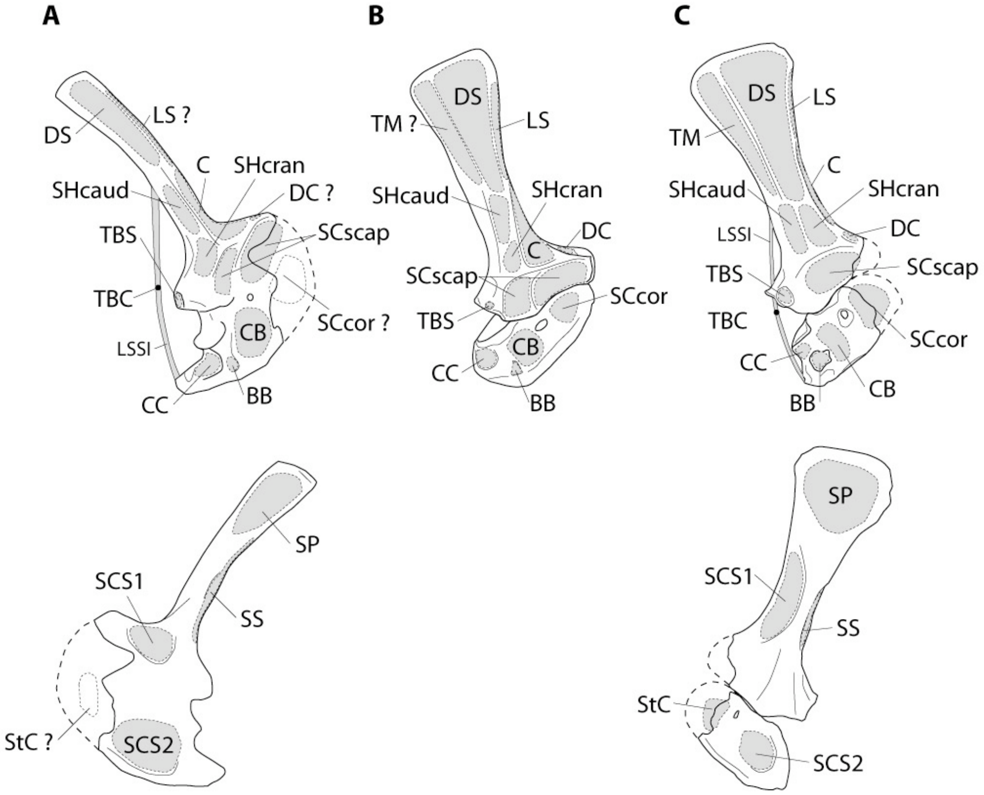

Figure 5-13. Reconstructions of the muscular attachments on the scapulocoracoid in *Herrerasaurus* (A), *Eoraptor* (B), and *Dilophosaurus* (C). Above, lateral view; below, medial view. Not to scale. For explanations see text.

The unusual form of the scapular blade of *Herrerasaurus* reflects a strong modification of the attaching musculature. The area for attachment of M. deltoideus scapularis has significantly shrunk. Moreover, the fossa for the origin of M. subscapularis on the medial side has shifted onto the scapular head, somewhat caudal to the acromial region (fig. 5-13). However, the osteological correlates of Mm. serrati and M. subcoracoideus on the scapula remain in a configuration similar to that of *Lewisuchus*. Like in *Eoraptor*, the area caudal to the facet for M. cucullaris on the lateral side of the proximal blade is very narrow. This implies a proximodistal configuration of the two Mm. scapulohumerales, under the assumption that both muscles preserved their independence. The subdivision of the fossa for M. supracoracoideus on the scapular head resembles *Eoraptor*, too, and may indicate a differentiation of this muscle into two individual heads. The enormous subglenoid fossa implies an unusually well developed M. costocoracoideus. The position and size of the biceps tubercle on the coracoid is, like in *Eoraptor*, more cranially placed than in the basal forms. The configuration of the sternoscapular ligament resembles *Lewisuchus*, and therefore implies a similar origin of M. triceps brachii caput coracoscapulare.

In *Dilophosaurus*, the clear differentiation of the lateral side of the scapular blade probably indicates the presence of a M. teres major. The configuration of the remaining muscles appears conservative, and closely resembles *Lewisuchus*: The sickle-shaped facet on the proximocranial scapular blade correlates to the attachment of M. cucullaris. The proximal quarter of the lateral side of the blade would have been shared by Mm. scapulohumerales, pars cranialis cranially and pars caudalis caudally. Differences are the exceptionally strong development of the tubercle for the origin of M. triceps brachii caput scapulare on the scapula, and of the tubercle correlating to the origin of M. biceps brachii on the coracoid. Lastly, the reduction of the subglenoid fossa is also a derived character.

Humerus (fig. 5-14). As for the scapulocoracoid, the relatively poor preservation of the bone surface in *Eoraptor* hampers the delimitation of muscle attachment sites. The flattened area proximoventrally on the humerus, caudal to the deltopectoral crest, probably served for the attachment of M. coracobrachialis, like in other tetrapods. The differentiation of the apex of the deltopectoral crest into a proximal and a distal facet may correlate to the differentiation of the fossa for M. supracoracoideus on the scapula. However, phylogenetic inference leaves the question unresolved what part of M. supracoracoideus inserted on which facet of the apex. The remaining muscles are reconstructed according to their phylogenetically inferred position, but no unambiguous osteological correlates allow for their exact delimitation. This is especially true for the (expectedly) tendinous origins of the entepicondylar muscles. The caudodistal facet of the humerus, next to the ulnar condyle, is assumed here to have served for the origin of M. flexor digitorum longus (see also chapter 6). However, there are also other possibilities, e.g. a correlation of this structure with the origin of M. entepicondylo-ulnaris.

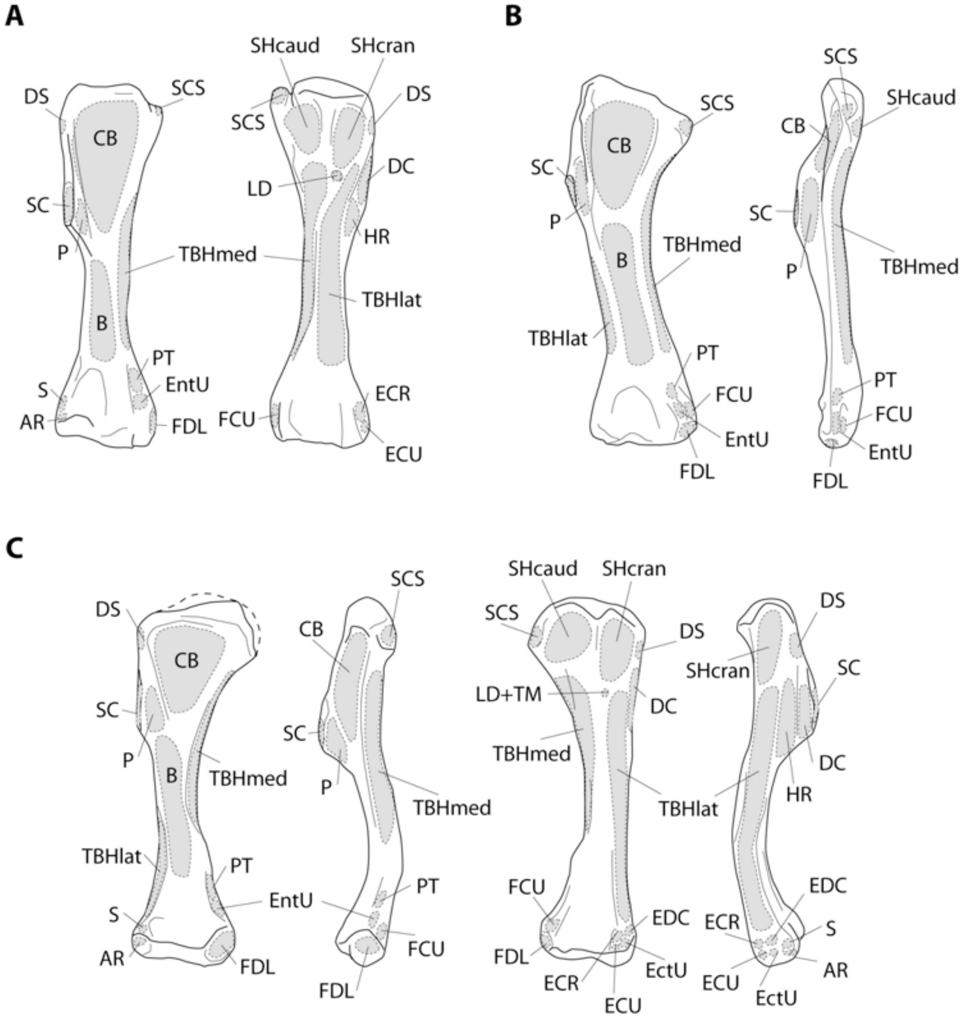

Figure 5-14. Reconstructions of the muscular attachments on the humerus of *Herrerasaurus* (A; left, ventral view; right, dorsal view), *Eoraptor* (B; left, ventral view; right, caudal view), and *Dilophosaurus* (C; from left to right, ventral, caudal, dorsal, and cranial views). Not to scale. For explanations see text.

Herrerasaurus is characterized by the unusual shape of the medial tuberosity, which nevertheless served for the insertion of M. subcoracoscapularis, as in other archosaurs. On the dorsal side of the humerus, the clearly delimited facets on both sides of the humeral head probably indicate the attachment sites of Mm. scapulohumerales, like in *Euparkeria*. Distally to these facets, the relatively small, round scar marks the insertion of M. latissimus dorsi. Cranially, the swelling proximal to the deltopectoral crest probably correlates to the insertion of M. deltoideus scapularis, while M. deltoideus clavicularis inserted on the cranial side of the crest. The distinct ridge between the crest and the dorsal side of the humerus marks the latter attachment. The differentiation of the elongate shaft into a dorsocranial and a caudal facet reflects the origins of M. triceps brachii caput humerale laterale and caput humerale mediale, respectively. There is no clear indication for M. humeroradialis on the humerus, but the rugose tubercle proximolaterally on the radius that probably correlates to the insertion of this muscle (chapters 3, 4; fig. 5-15), strongly speaks for its presence in *Herrerasaurus*. On the ventral side, the strong striations on the caudal side of the deltopectoral crest indicate the insertion of M. pectoralis. More distally, the ventral shaft probably served for the origin of M. brachialis, like in other archosaurs. The enlarged entepicondyle provides much room for the origins of M. pronator teres and M. entepicondylo-ulnaris. Moreover, the distocaudal facet of the humerus is enlarged relative to *Eoraptor*, possibly indicating a stronger developed tendon of origin of M. flexor digitorum longus. Other epicondylar muscles have no unambiguous osteological correlates and are reconstructed in a generalized reptilian pattern.

Considering muscle attachment sites, the humerus of *Dilophosaurus* is not significantly different from basal saurischians. The most marked exemption is the enlargement of the caudodistal facet, probably indicating an even stronger development of M. flexor digitorum longus. In addition, the scar for the insertion of M. latissimus dorsi and M. teres major on the dorsal side of the shaft cannot be recognized, and may have been only weakly developed.

Antebrachium (figs. 5-15, 5-16). The inferred sites of muscular attachment on the radius are similar in *Eoraptor, Herrerasaurus*, and *Dilophosaurus* (fig. 5-15). The medial side is more or less clearly differentiated into a cranial and a caudal facet, the former serving for the attachment of M. pronator teres, the latter for that of M. pronator quadratus. On the lateral site, there is a similar differentiation, reflecting the attachment sites of M. supinator cranially, M. supinator manus caudally, and M. abductor radialis caudoproximally.

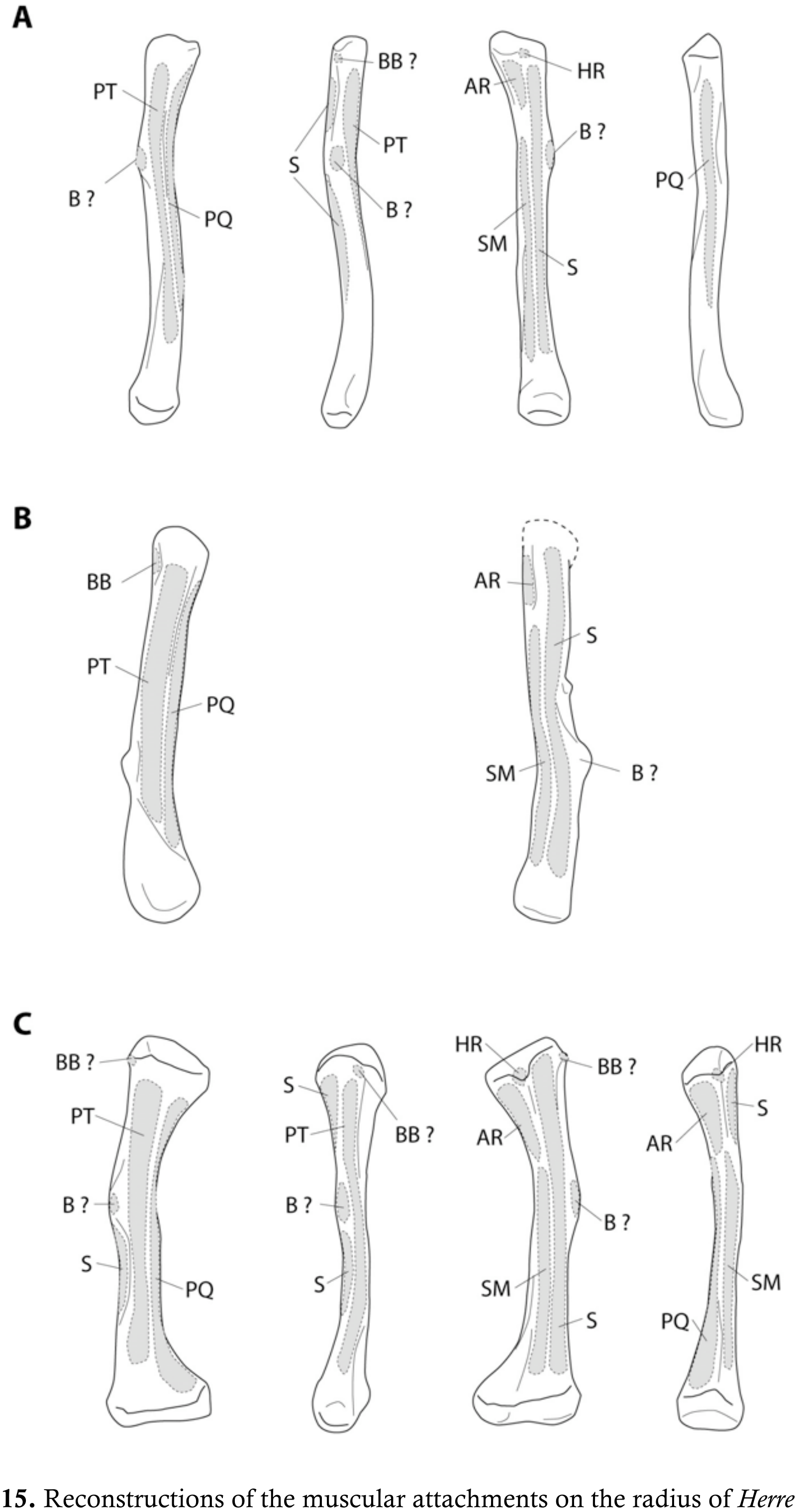

Figure 5-15. Reconstructions of the muscular attachments on the radius of *Herrerasaurus* (A), *Eoraptor* (B), and *Dilophosaurus* (C). From left to right, medial, cranial, lateral, and caudal views. Not to scale. For explanations see text.

The large tubercle cranial on the radius has usually been interpreted as the site of insertion of M. biceps brachii (e.g., Smith and Carpenter, 1990; Sereno, 1993). The proximolateral tubercle consequently served for the insertion of M. humeroradialis. In *Eoraptor*, a tubercle resembling the 'biceps tubercle' of the other forms is placed far too distally to make a realistic site of insertion of this muscle (compare fig. 5-23; Discussion). If this tubercle were homologous to the 'biceps tubercle', an alternative muscle configuration would be necessary. One possibility is that the strong connection between M. brachialis and M. biceps brachii was given up in basal saurischians, making a more distal insertion of M. brachialis on the antebrachium possible, while M. biceps brachii kept its plesiomorphic insertion cranioproximally on radius and ulna (fig. 5-24). A second option would be that M. humeroradialis shifted its insertion distally and attached to the tubercle under consideration, but again the position of this tubercle in *Eoraptor* would produce an unrealistic line of action (see Discussion below).

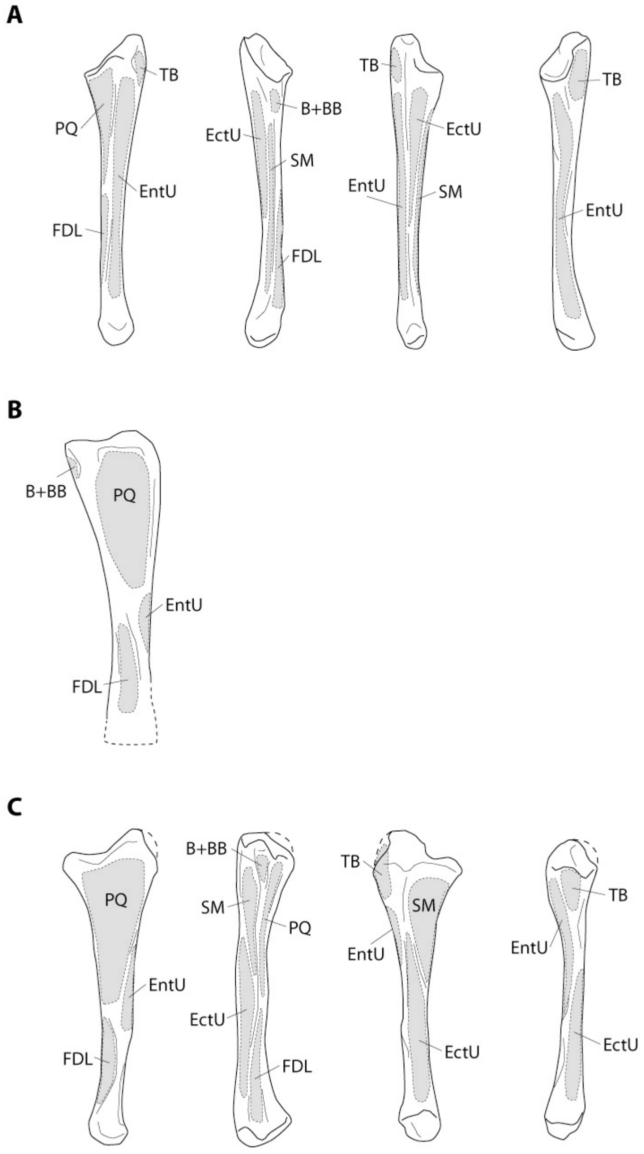

Figure 5-16. Reconstructions of the muscular attachments on the ulna of *Herrerasaurus* (A), *Eoraptor* (B), and *Dilophosaurus* (C). From left to right, medial, cranial, lateral, and caudal views. Not to scale. For explanations see text.

The ulnae (fig. 5-16) of basal saurischians have comparable myological patterns, but differences are more marked than in the radius. The swelling at the tip of the cranial process probably served for insertion of the M. biceps brachii / M. brachialis system (but see Discussion below), while the strongly striated facet on the caudoproximal side indicates the attachment of the M. triceps brachii complex. The depression or facet proximally on the medial shaft marks the origin of M. pronator quadratus; this correlate is somewhat reduced in size in *Herrerasaurus*. The distomedial facet probably served for the origin of the ulnar head of M. flexor digitorum longus, while the striated caudal side of the shaft indicates the insertion of M. entepicondylo-ulnaris. However, the latter two muscles have no unambiguous osteological correlates (chapter 3), rendering their delimitation somewhat speculative. An intermuscular crest subdivides the lateral side of the ulna, separating M. entepicondylo-ulnaris caudally and M. ectepicondylo-ulnaris cranially. The cranial edge of the radius probably served for the radial origin of M. supinator manus. In *Dilophosaurus*, the subtriangular depression cranioproximally on the lateral side may indicate a proximal extension of this latter muscle (fig. 5-16C).

Manus. In the proximal carpus, tubercles dorsomedially on the ulnare and dorsolaterally on the radiale probably indicate the insertion of M. extensor carpi radialis and M. extensor carpi ulnaris, respectively. The facet proximomedially on the ventral side of the ulnare marks the insertion of M. pronator quadratus. Distally to this facet, a small depression possibly indicates the origin of M. abductor pollicis brevis. The pisiforme, if preserved, correlates to the attachment of M. flexor carpi ulnaris. The proximolateral flanges of the metacarpals are interpreted here as sites of insertion of the tendons of M. extensor digitorum communis. Like in other Reptilia, the depressions on the dorsal side of the metacarpals represent the origin of Mm. extensores digitorum profundi, while similar depressions on the ventral side correlate with the origin of Mm. flexores digitorum profundi (chapter 3). The extensor tubercles of the phalanges most likely connected to the shared tendons of Mm. extensores digitorum superficiales and Mm. extensores digitorum profundi. The origins of the Mm. extensores digitorum superficiales probably were located on the carpus, but their exact pattern is a matter of speculation. The ungual flexor tubercles correlate with the insertions of the tendons of M. flexor digitorum longus. Based on phylogenetic inference, there was probably also a M. flexor digitorum superficialis that arose from a palmar aponeurosis and inserted on the phalangeal flexor tubercles (chapter 3). However, the exact configuration of such a muscle has to remain speculative. Since Mm. interossei and Mm. lumbricales lack unambiguous correlates, and phylogenetic inference of the basal archosaurian pattern is also difficult in this case (chapter 3), no attempt to reconstruct these muscles is made here.

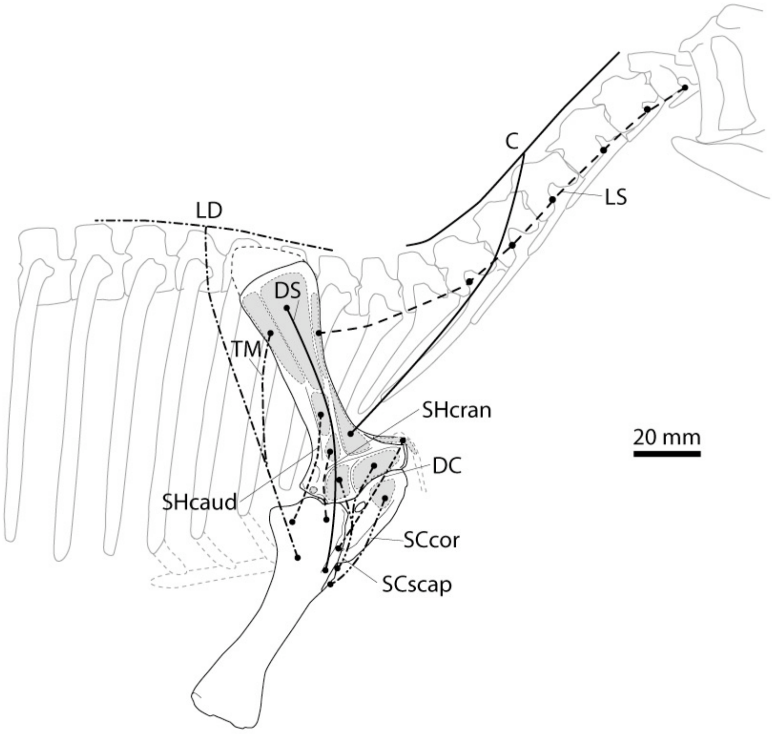

Figure 5-17. Reconstruction of the skeletomuscular system of the shoulder girdle of *Eoraptor* (superficial part) in lateral view. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle.

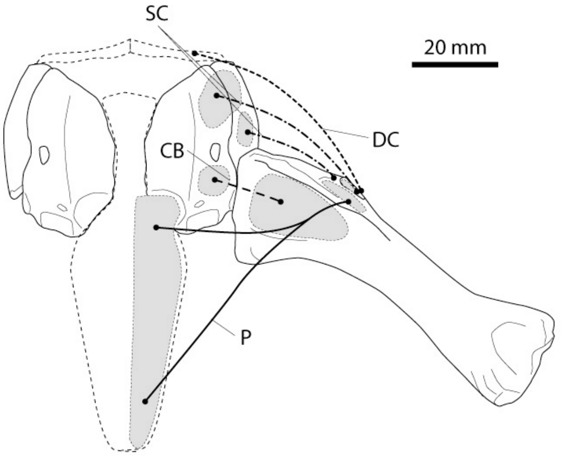

Figure 5-18. Reconstruction of the skeletomuscular system of the shoulder girdle of *Eoraptor* in ventral view. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle.

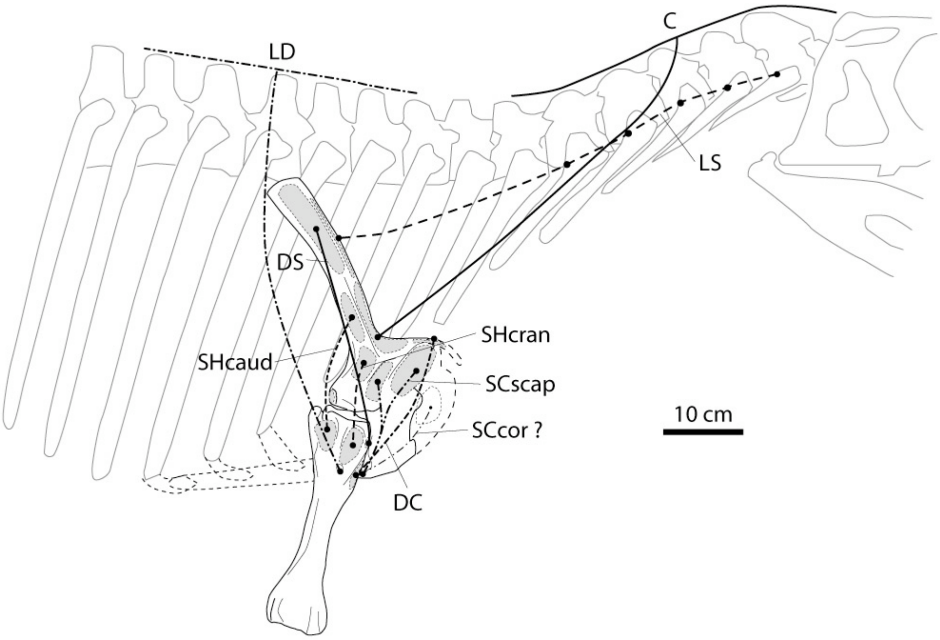

Figure 5-19. Reconstruction of the skeletomuscular system of the shoulder girdle of *Herrerasaurus* (superficial part) in lateral view. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle.

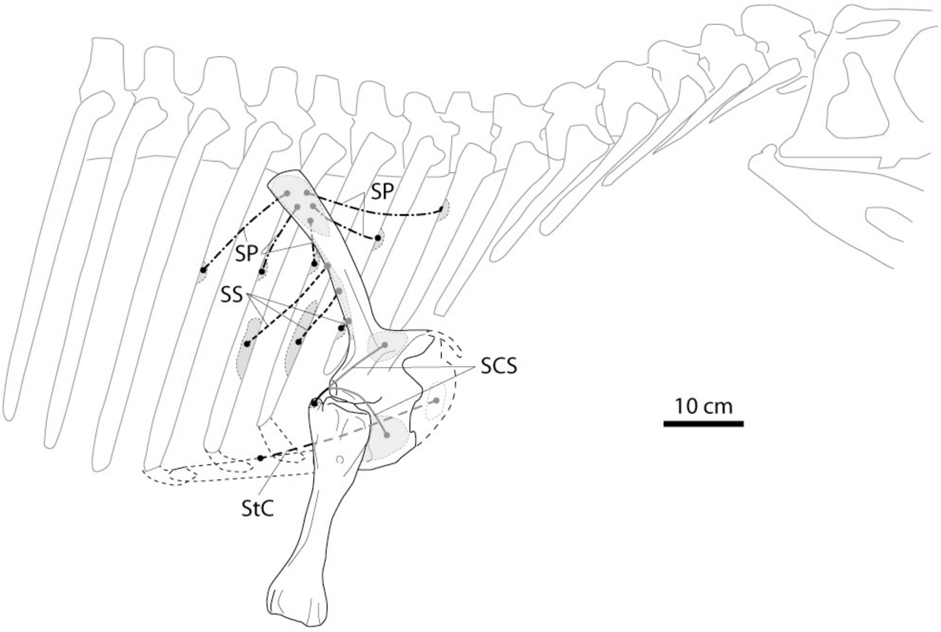

Figure 5-20. Reconstruction of the skeletomuscular system of the shoulder girdle of *Herrerasaurus* (deep part) in lateral view. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle.

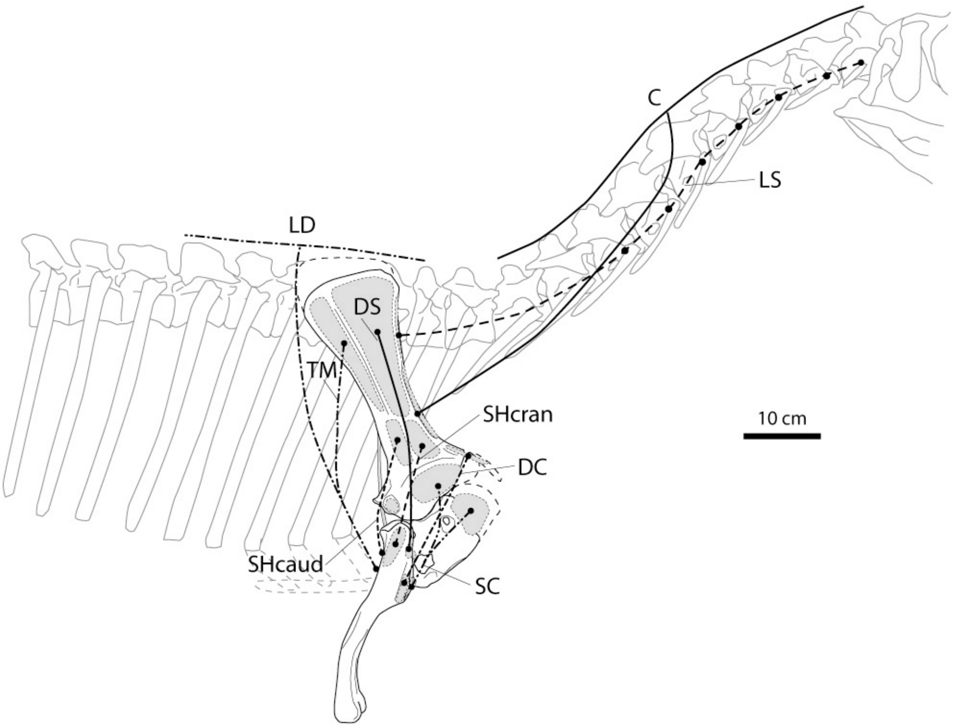

Figure 5-21. Reconstruction of the skeletomuscular system of the shoulder girdle of *Dilophosaurus* (superficial part) in lateral view. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle.

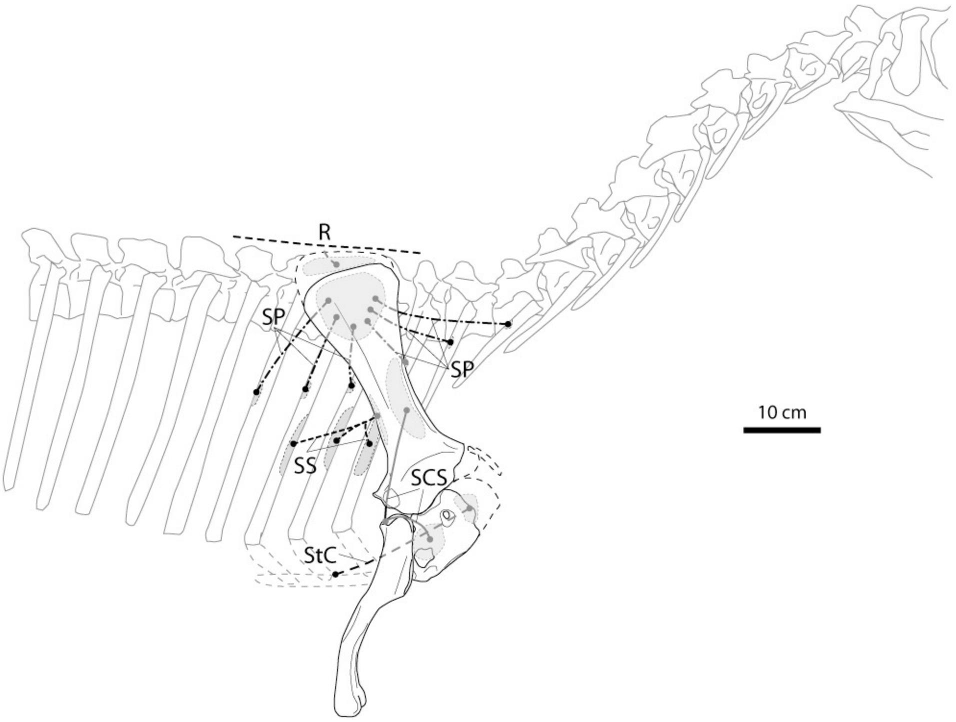

Figure 5-22. Reconstruction of the skeletomuscular system of the shoulder girdle of *Dilophosaurus* (deep part) in lateral view. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle.

Discussion

Shoulder region

Reconstructions of the skeletomuscular systems of the shoulder region of *Eoraptor*, *Herrerasaurus*, and *Dilophosaurus* (figs. 5-17 to 5-22) exhibit a relatively high grade of correspondence among these forms, despite the deviant morphology of the scapular blade in *Herrerasaurus*. To maintain effective lines of action for M. levator scapulae and M. cucullaris, the scapular blade has to be inclined 60–70° against the horizontal in all three genera. The Mm. serrati would be anchored primarily on the first 3–4 dorsal ribs. In *Herrerasaurus,* the main difference to other basal dinosaurs is the position of M. subscapularis. The cranioventral shift of its origin relative to the pivot it acts on (the shoulder articulation) causes a change in function: Instead of assisting in retraction of a subhorizontally oriented humerus (the plesiomorphic function), the novel course leads to an outward rotation of the humerus around its long axis when the muscle contracts. In combination with protraction, this would bring the hands into a position more suitable for grasping, despite the caudolateral orientation of the glenoid (see also the following paragraph). Theropods like *Dilophosaurus* lack this adaptation because they developed a different solution: M. subscapularis kept its plesiomorphic position medially on the scapular blade, but the glenoid is reoriented caudalwards, rendering the muscle an adductor instead of a retractor. The reduction of the scapular blade in *Herrerasaurus* actually may be a direct consequence of the shift of M. subscapularis. The course of M. deltoideus clavicularis is hard to reconstruct in the three genera considered here, since no clavicles are preserved. However, *Dilophosaurus* most likely had a wide V-like furcula (as known from coelophysoids and basal tetanurans) that did not extend far cranioventrally. Under consideration of the form of the scapulocoracoid, the line of action of M. deltoideus clavicularis appears therefore to be more vertically oriented than in more basal forms, probably correlating to a more vertically held humerus (see below). The remaining muscles do not show many modifications relative to *Lewisuchus* (see chapter 4). This combination probably allowed for a high grade of movement variability, including protraction and retraction when the humerus was more or less strongly abducted from the parasagittal plane.

In addition to the reduced scapular blade of *Herrerasaurus,* the most marked osteological differences among the taxa examined here can be observed in the humerus. These include variable grades of overall robustness, and differing lengths of the deltopectoral crest. The relatively longest crests (with up to 50%

humerus length) are found in the basal forms, *Guaibasaurus* (Bonaparte et al., 2007) and *Eoraptor*. The proximal humeral expansion exhibits additional differences: In *Eoraptor*, the craniocaudally wide but dorsoventrally narrow humeral head lacks an extension onto the ventral side of the shaft, and is therefore best suited for rotational movements in (developmentally) craniocaudal, but not dorsoventral directions. In combination with the wide, caudolaterally opening glenoid, this form implies a relatively great flexibility in the movements of the humerus, but excludes an upright, parasagittal swinging. The same conclusions apply also to *Herrerasaurus*. In *Dilophosaurus*, the combination of a large, vaulted humeral head that extends both on the developmentally ventral and dorsal sides of the humerus, with a more caudally directed glenoid that has an enlarged scapular portion and a reduced coracoidal portion, implies a humeral neutral position with a more cranially oriented deltopectoral crest. Moreover, this would create the possibility to retract the humerus relatively far, in a near-parasagittal plane. The forward deflection of the distal end, as well as the caudal inclination of the medial tuberosity relative to the main axis of the proximal end, may also correlate to this alternate posture of the humerus. In addition, a more vertical position of the humerus apparently led to a reduction of the size of the deltopectoral crest. This may be explained by the resulting new function of M. latissimus dorsi / M. teres major and Mm. scapulohumerales in retracting the humerus, which probably led to a loss of importance of M. pectoralis.

Arm

The most significant differences among the brachial skeletomuscular systems of the taxa examined here are found in the distal humerus, and much less so in the forearm. The widely spaced distal condyli of the humerus in *Eoraptor* indicate that ulna and radius could easily be rotated against each other, while the narrow, compressed distal articulation in *Dilophosaurus* probably caused less flexibility in this joint. In *Eoraptor* and *Herrerasaurus*, the ulnar condyle is significantly larger than the corresponding cotyle of the ulna, also indicating good rotational capabilities. In *Eoraptor,* both condyli are not oriented in parallel, but form a ventrally concave arc. In contrast, *Herrerasaurus* exhibits a ventrally convex arc. The resulting rotational axes of the articular surfaces would have supported pronation of the hand in *Eoraptor*, but supination in *Herrerasaurus*.

Another prominent difference is the presence of a large intercondylar pit on the developmentally ventral side of the humerus of *Eoraptor*. Such a pronounced pit is lacking in herrerasaurids and theropods, but is present in *Euparkeria* (chapter 4) and basal sauropodomorphs (chapter 6). Like in living tetrapods, the ventral intercondylar pit was covered by the articular capsule and stored synovial fluid (see Gardner, 1950; MacConnaill, 1950). Probably, a great amount of synovial fluid was needed to be stored within the capsule when changing compressive loads acted on the joint and pressed the fluid out of the cartilage (weeping lubrication: McCutchen, 1983; Myers, 1983). Compressive loads would occur if the limb was used for locomotion, but not during grasping movements. Since a parasagittal posture of the humerus can be excluded (see above), the presence of a ventral intercondylar pit may be interpreted as evidence for facultative quadrupedal locomotion in *Eoraptor*, with the humerus held in a semi-erect posture. In turn, the reduction of this depression in *Herrerasaurus* and theropods correlates to obligate bipedalism.

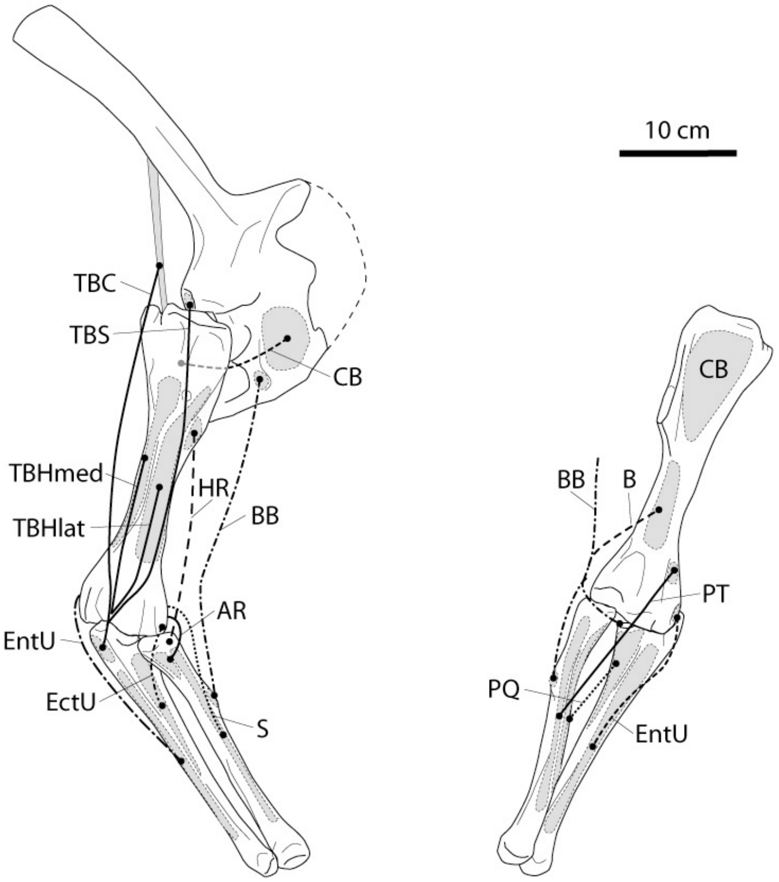

Figure 5-23. Reconstruction of the skeletomuscular system of the arm of *Herrerasaurus* in dorsolateral (left) and ventromedial (right) views. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle.

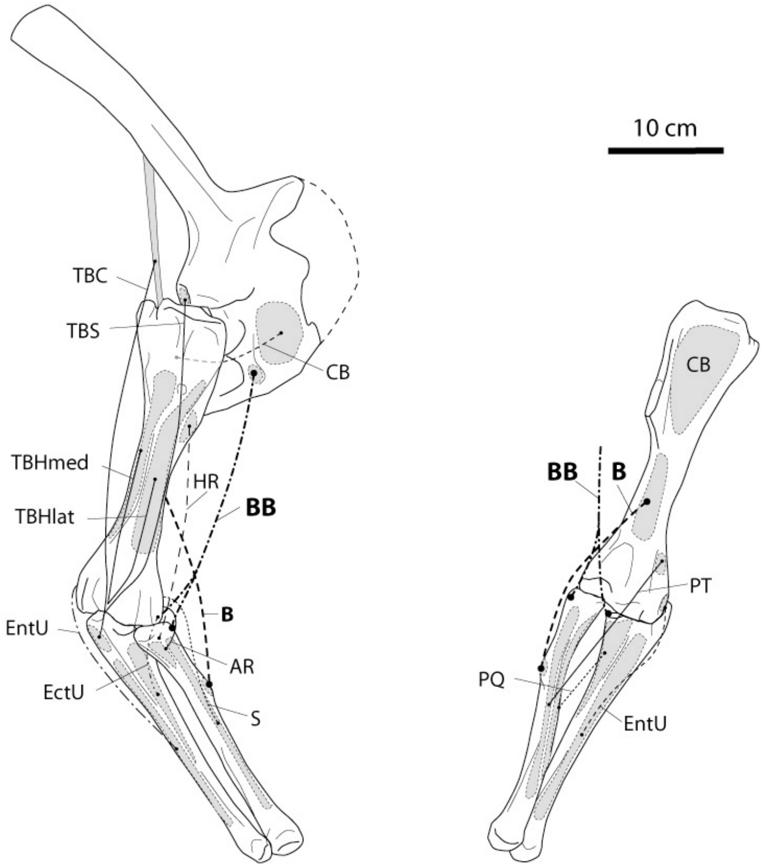

Figure 5-24. Alternative reconstruction of the M. biceps brachii / M. brachialis system in *Herrerasaurus*. For explanations see text.

As mentioned above, differences in the antebrachium mainly pertain to varying positions of the ‘biceps tubercle’ of the radius. Assuming that M. biceps brachii indeed inserted on this tubercle, the resulting line of action would run far cranial to the humerus, producing an unrealistic gap between muscle and bone. Since M. biceps brachii is a two-joint muscle, its effectiveness in flexing the forearm may actually have been reduced by such a configuration (see also Bock, 1968): Contraction of M. biceps brachii would have caused the humerus to rotate caudally, depending on the angle of humeral abduction. Moreover, a distal placement of the insertion of M. biceps brachii would make an extraordinary elongation of this muscle necessary during forearm extension. These problems are avoided if the M. biceps brachii / M. brachialis system is reconstructed similar to other non-avian reptiles, with both muscles fusing distally, then splitting again to attach by tendons cranially to both ulna and radius (figs. 5-23, 5-25). In this case, the distal shift of the tubercle on the radius would make both muscles to cause not only flexion of the elbow joint during contraction, but also to pronate the hand. However, such a construction appears not to be very effective. The alternative model proposed above (fig. 5-24), with separated M. biceps brachii and M. brachialis (the latter inserting alone on the radial tubercle) would provide efficient lines of action for both muscles: M. biceps brachii remains the primary flexor of the antebrachium and avoids undesirable movements of the humerus by running in parallel to the humeral shaft axis, while M. brachialis becomes a strong pronator of the hand. Assuming that *Eoraptor* was capable of quadrupedal locomotion (see above), the distal position of the radial tubercle in this taxon consequently might have allowed for full pronation of the hand, in order to place it firmly on the ground. However, such a system would be a novelty not known from any living reptile (chapter 3). Therefore, quantitative biomechanical analyses and computer models (which are beyond the scope of the present work) are the only way to assess if the model proposed here might be a realistic option. Future research in this direction will probably lead to a more complete understanding of forearm functions of early dinosaurs.

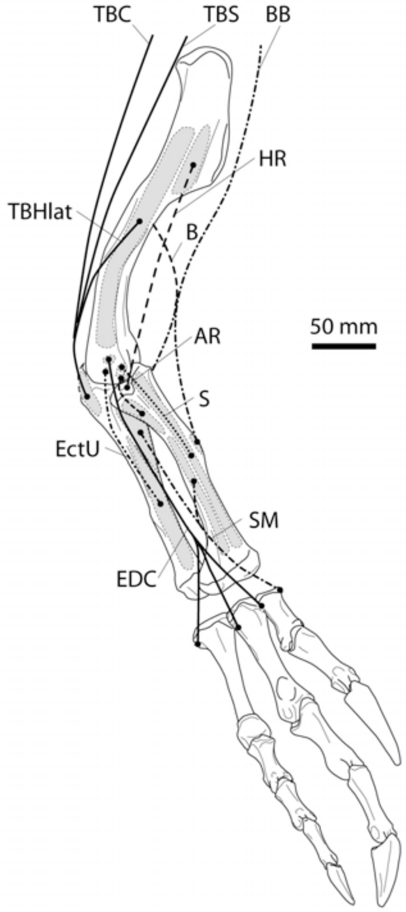

Figure 5-25. Reconstruction of the skeletomuscular system of the arm of *Dilophosaurus* in dorsolateral view. Muscles are depicted by their estimated lines of action, giving a gross idea of the function of each muscle.

Regarding the ulna, it is interesting to note that *Eoraptor* (and also *Guaibasaurus*) apparently lack a distinct olecranon process, while this feature is pronounced in *Herrerasaurus* and basal eutheropods. The olecranon process is a lever that transfers pulling forces of the M. triceps brachii complex onto the ulna. Possibly, its prominence in these early bipedal predators allowed for more effective raking movements by forceful extension of the forearm.

Manus

The inference of facultative quadrupedalism in *Eoraptor* from humeral and antebrachial morphology (see above) is also supported by the anatomy of the hand. Concluding from the presence of ligament pits, metacarpal IV probably articulated with a fully developed proximal phalanx. Given the phylogenetic position of *Eoraptor* as the sister taxon to Sauropodomorpha + Theropoda (Langer, 2004; Langer and Benton, 2006), it is likely that this form possessed at least two phalanges in digit IV, like many basal sauropodomorphs. The medial rotation of the distal end of metacarpal IV may have helped to place the digit on the ground during quadrupedal locomotion, but without data about the morphology of the phalanges of digit IV, this assessment is rather speculative.

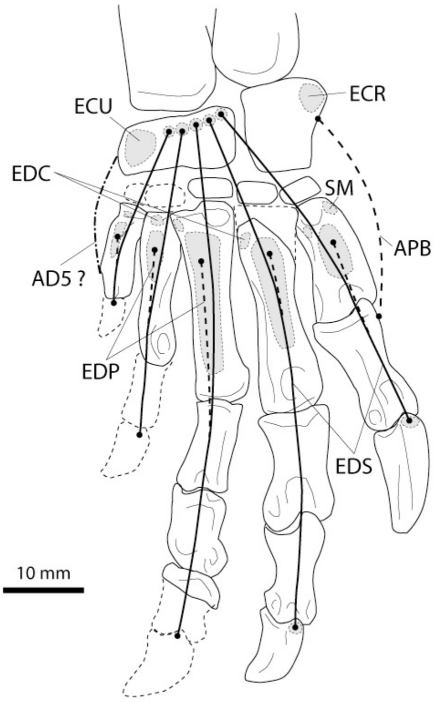

Figure 5-26. Reconstruction of the intrinsic muscles of the hand of *Eoraptor* in dorsal view. Muscles are depicted by their estimated lines of action, giving a gross idea of the function of each muscle.

Extensor pits on the distal ends of the metacarpals are present in all early dinosaurs (including heterodontosaurids), but their strong development in theropods like *Dilophosaurus* obviously is related to an increased capability of digital hyperextension (Galton, 1971b; Raath, 1977; see also Carpenter, 2002). In *Eoraptor*, the form of the unguals is generalized: they appear neither especially adapted to predation nor to locomotion. In contrast, the elongate, strongly recurved unguals of *Herrerasaurus* and *Dilophosaurus* demonstrate adaptations for grasping and raking in these taxa (Welles, 1984; Sereno, 1993). The elongation of the digits and reduction of the outer fingers in these predatory forms supports such an interpretation of manus function.

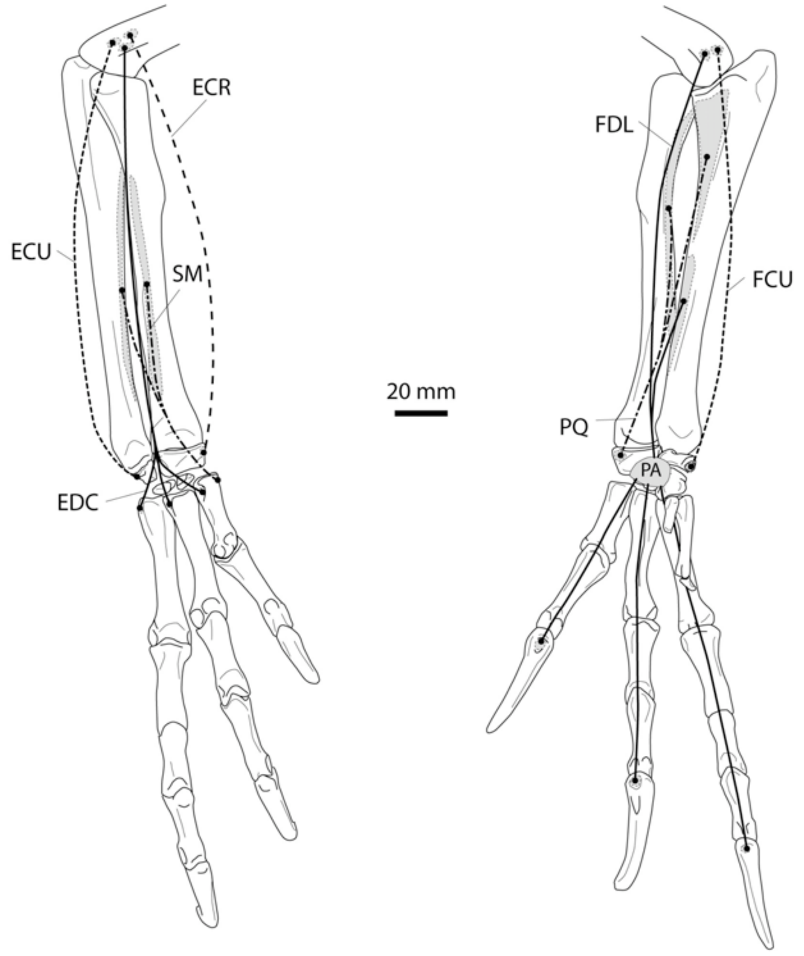

Figure 5-27. Reconstruction of the forearm muscles acting on the hand of *Herrerasaurus* in dorsal (left) and ventral (right) views. Muscles are depicted by their estimated lines of action, giving a gross idea of the function of each muscle.

Despite these osteological novelties, the inferred muscular system of the hand exhibits no obvious modifications of the plesiomorphic pattern (figs. 5-26, 5-27, 5-28). Where observable, the insertions of the epicondylar extensors and flexors on the carpus are conservative. The same is true for the configuration of the intrinsic extensors and flexors of the hands of *Eoraptor, Herrerasaurus,* and *Dilophosaurus*. Possible specializations of the intrinsic abductors and adductors that may be related to the asymmetry of digit I cannot be recognized, due to the lack of unambigous osteological correlates (chapter 3).

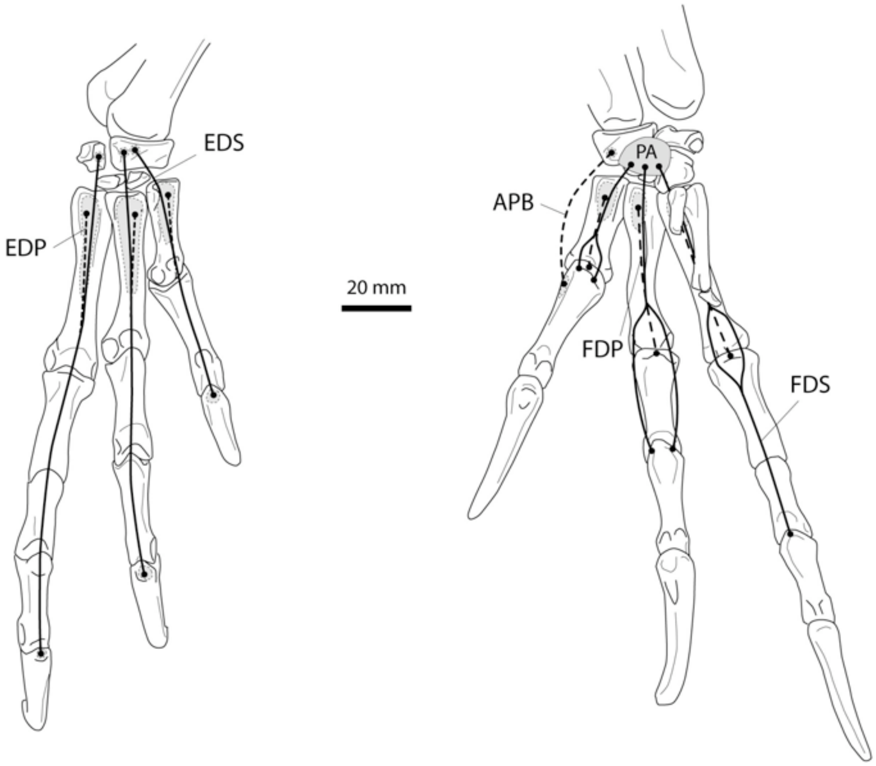

Figure 5-28. Reconstruction of the intrinsic hand muscles of *Herrerasaurus* in dorsal (left) and ventral (right) views. Muscles are depicted by their estimated lines of action, giving a gross idea of the function of each muscle.

<u>Body proportions</u>

Measurements of limb element and trunk lengths of several basal dinosaurian taxa are summarized in table 1. In *Herrerasaurus*, *Guaibasaurus*, and *Liliensternus*, the trunk length estimate is based on the preserved dorsal vertebrae. This was also done for *Eoraptor*, but due to the state of preservation of PVSJ 512, the number of dorsal vertebrae cannot be assessed reliably. The observable dorsal centra measure about 22 mm in length. Assuming there were 15 dorsal vertebrae as in other basal dinosaurs, the original trunk length may have been around 340 mm. The lengths of the forelimb elements of *Guaibasaurus* were calculated based on the proportions of the newly found specimen published by Bonaparte et al. (2007).

Taxon	DVL	SL	HL	RL	MC3L	FL	TL	MT3L
Eoraptor	340*	81	84	60	21	156	160	77
Herrerasaurus	560*	273	175*	153	57	345	315	165
Guaibasaurus	470*	128	110*	67*	27*	214	212	95
Liliensternus	650*	300	205	150	68	420	400	220
Dilophosaurus	896	331	283	283	98	557	553	300
Heterodontosaurus	172	86	83	58	22	112	145	68

Table 1. Morphometric measurements of several basal dinosaurs. All values are given in mm. Abbreviations: **DVL**, length of dorsal vertebral column; **SL**, scapula length; **HL**, humerus length; **RL**, radius length; **MC3L**, length of metacarpal III; **FL**, femur length; **TL**, tibia length; **MT3L**, length of metatarsal III. Asterisks (*) indicate extrapolations that were necessary because of incomplete preservation.

Based on these values, general body and limb proportions are calculated and listed in table 2. It becomes evident that among basal saurischians, *Eoraptor* has an unusually large humerus in relation to the scapula, and a hind limb to trunk length ratio well below that of herrerasaurids and eutheropods. According to empirical observations made first by Galton (1976a), a value of this ratio above 1.2 is indicative for obligate bipedalism, while values below 0.9 are found in obligate quadrupeds. Like many basal sauropodomorphs (Galton, 1976a), *Eoraptor* and *Guaibasaurus* range between these values. Hence, body proportions independently support the interpretation that *Eoraptor,* and possibly also *Guaibasaurus,* were capable of facultative quadrupedalism.

Taxon	FLL	HLL	HL/SL	FLL/HLL	HLL/DVL
Eoraptor	165	393	**1.04**	0.42	**1.15**
Herrerasaurus	385	825	0.64	0.47	1.47
Guaibasaurus	204	523	**0.86**	0.39	**1.12**
Liliensternus	655	1040	0.68	0.63	1.59
Dilophosaurus	664	1410	0.85	0.47	1.56
Heterodontosaurus	163	325	0.97	0.50	1.89

Table 2. Limb and trunk proportions in basal dinosaurs. Abbreviations: **FLL**, total forelimb length (= combined lengths of humerus, radius, and metacarpal III); **HLL**, total hind limb length (= combined lengths of femur, tibia, and metatarsal III); **HL/SL**, humerus to scapula length; **FLL/HLL**, forelimb to hind limb length; **DVL/HLL**, trunk to hind limb length.

Conclusions

Although phylogenetically more closely related to Theropoda and Sauropodomorpha than *Herrerasaurus* (Langer, 2004; Langer and Benton, 2006; fig. 5-1), *Eoraptor* exhibits a much more plesiomorphic *bauplan* of the pectoral girdle and forelimb, closely resembling *Lewisuchus* where comparisons can be made. Both osteologically and myologically, the forelimb anatomy of *Eoraptor* shows adaptations suited for quadrupedal locomotion. These characters are plesiomorphic, and not secondarily acquired. However, the elongate hindlimbs and dorsoventrally high torso (as demonstrated by the shape of the pectoral girdle) inherited from forms like *Lewisuchus* are indicative for cursorial abilities. Naturally, the preferred mode of locomotion of *Eoraptor* in life is a matter of behavior, and cannot be inferred from anatomy alone.

As demonstrated by the totally different solutions for protracting and supinating the hands in *Herrerasaurus* and theropods such as *Dilophosaurus*, it is most probable that herrerasaurids acquired obligate bipedality independently. It can be confirmed that this group constitutes a highly specialized branch of early dinosaurs that has no tight relations to any other dinosaurian clade (Holtz, 1995a; Langer, 2004; Langer and Benton, 2006). Therefore, evolutionary transformations of the hind limbs and forelimbs of early dinosaurs have been independent processes (see also chapter 9). All neotheropods are obligate bipeds with grasping adaptations in the arm and hand, but basal theropods preserve a conservative, dinosauriform-like pectoral girdle.

6 The pectoral girdle and forelimb of basal sauropodomorphs: Anatomy and functional interpretation

Introduction

As has been shown in the previous chapter, the hypothesis of an obligate bipedal ancestor of all dinosaurs (Sereno, 1991, 1997) is seriously questioned by a thorough study of the anatomy of the basal saurischian *Eoraptor lunensis*. Proportions and hind limb anatomy (Langer, 2004; Fechner, in prep.) are compatible with facultative quadrupedalism. Moreover, the relatively plesiomorphic forelimb anatomy exhibits adaptations to locomotion, but not to grasping as would be expected for obligate bipeds. Recent discoveries of the basal-most theropod known, *Guaibasaurus candelariensis* (Bonaparte et al., 2007), imply that facultative quadrupedalism may still have been possible at the root of the predatory dinosaurs (chapter 5). Since both the sister taxon and the outgroup to Sauropodomorpha are originally no obligate bipeds, the question for the ancestral forelimb *bauplan* and type of locomotion in sauropodomorphs is pending. Key taxa for an understanding of this issue are the basal sauropodomorphs *Saturnalia tupiniquim*, *Thecodontosaurus antiquus, Pantydraco caducus*, and *Efraasia minor*, which will be addressed in the chapter at hand. In recent phylogenetic analyses, these taxa stand outside the clade comprising plateosaurids and more derived sauropodomorphs (including sauropods), i.e. the Anchisauria of Upchurch et al. (2007), or the Plateosauria of Yates (2007). The position of *Mussaurus* among basal sauropodomorphs is uncertain (Galton and Upchurch, 2004; Upchurch et al., 2007), since this taxon is based only on early juvenile specimens. Therefore, *Mussaurus* will not be treated in this chapter, but comments on the forelimb anatomy of this form are included in chapter 7.

In contrast to *Eoraptor*, the forelimb anatomy of *Saturnalia*, *Thecodontosaurus*, *Pantydraco*, and *Efraasia* has been described in great detail by other authors (Galton, 1973, 1984; Benton et al., 2000; Yates, 2003; Galton et al., 2007; Langer et al., 2007). Based primarily on hindlimb anatomy, Langer (1999, 2003) claimed that *Saturnalia* was no obligate biped, but used a quadrupedal posture when moving slowly. Moreover, Langer et al. (2007) attempt to reconstruct forelimb muscle attachments in *Saturnalia*. However, the myological results of Langer et al.'s (2007) work are problematic in several respects:

- for the reconstruction of the shoulder girdle musculature, none of the muscles that connect the girdle to the axial skeleton (M. cucullaris, M. levator scapulae, Mm. serrati, M. costocoracoideus, M. sternocoracoideus) were considered;
- names and subdivisions of muscles are based on a comparison of crocodilian and avian anatomy only, leading to the reconstruction of muscles that probably were not present in basal archosaurs (see chapter 3);
- many structures are 'over-interpreted': although there are countless cracks, fragmentations, and abrasions in the material, minute structures are homologized with avian characters, or figured as insertion sites of certain muscles without discussing the probability of these inferences;
- some of the inferences made are highly unrealistic, e.g. the identification of the ventral intercondylar pit of the distal humerus (which was located inside the articular capsule) as the point of origin of M. brachialis;
- and finally, all inferences are discussed under topological comparisons to birds and crocodylians only, but not under functional considerations.

Therefore, the present chapter reassesses the skeletomuscular system of *Saturnalia* with the method developed in chapter 3, but describes only additional observations and novelties that are significant for muscle reconstructions. Moreover, the anatomy of the pectoral girdle and forelimb of more derived basal sauropodomorphs (*Thecodontosaurus, Pantydraco,* and *Efraasia*) will be summarized and interpreted in terms of myological evolution, with an emphasis on the medium-sized form *Efraasia* from the Middle Norian of Germany. Phylogenetically, this genus represents the beginning of size increase in sauropodomorphs (fig. 6-1), and hence the first recorded step towards sauropod gigantism.

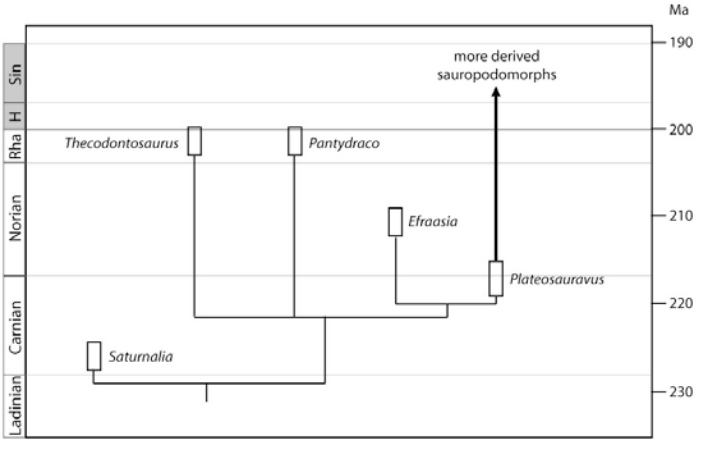

Figure 6-1. Relationships and temporal distribution of basal sauropodomorphs. Note the extensive gaps in the fossil record. Cladogramm simplified after Yates (2007).

Anatomy

Saturnalia tupiniquim

Scapula. In contrast to other basal dinosauriforms, the middle part of the scapular blade is considerably constricted with respect to both the distal expansion and the scapular head (fig. 6-2). The caudal third of the lateral side of the blade is craniocaudally convex, with the exemption of the caudodistal corner, which is slightly flattened. On the medial side of the base of the blade, a triangular depression extends distally beyond the craniocaudal center of the shaft. Like in other early dinosaurs, an elongate facet on the caudoproximal part of the medial side of the blade extends distally for about one third of the length of the shaft. The ridge that borders this facet cranially does not extend to the distal part of the blade (*contra* Langer et al., 2007); this area of the bone is entirely flat. As noted by Langer et al. (2007), a thickened, rugose distal edge of the blade indicates the presence of a cartilaginous suprascapula. Like in other basal dinosaurs, the fossa laterally on the scapular head (origin of M. supracoracoideus) extends far caudally and connects to the glenoid rim. Moreover, a distinct acromial crest resembling that of neotheropods (chapter 5) borders the cranial half of the fossa dorsally. Craniodorsal to this crest, an oval, rugose, dorsomedially facing tubercle indicates the clavicular articulation. In contrast to Langer et al. (2007), a 'coracoid tuber' could not be recognized; the structure mentioned by these authors is surrounded by fractures and may be an artefact, since it is missing in the scapula of the paratype (see also 'Muscle reconstructions' below). Caudally, the scar for the origin of M. triceps brachii caput scapulare ('supraglenoidal pit' of Langer et al., 2007) is found 4 mm dorsal to the edge of the glenoid, and is caudally and slightly laterally oriented. The suture between scapula and coracoid is fused. The course of the suture slightly curves craniodorsally, but misses the characteristical 'step' seen in *Eoraptor* and most theropods.

Coracoid. The coracoid of *Saturnalia* is characterized by a large subglenoid fossa on its caudal side (fig. 6-2). Langer et al. (2007) describe the form of this fossa in detail, which equals the coracoidal part of the glenoid in size. The main difference to other basal dinosaurs is the lack of a lateral ridge that separates the subglenoid fossa from the ventromedial (external) surface of the coracoid; a similar condition is found in *Dilophosaurus* (chapter 5). The semilunate biceps tubercle of *Saturnalia* is prominent (but not as large as in basal theropods), and situated cranially between the subglenoid fossa and a striated depression on the caudomedial corner of the coracoid. The dorsomedial (internal) side of the coracoid is strongly concave and exhibits intense striations that are craniomedially oriented. The coracoidal part of the glenoid is large relative to the scapular part, rendering the glenoid cavity caudoventrolaterally oriented.

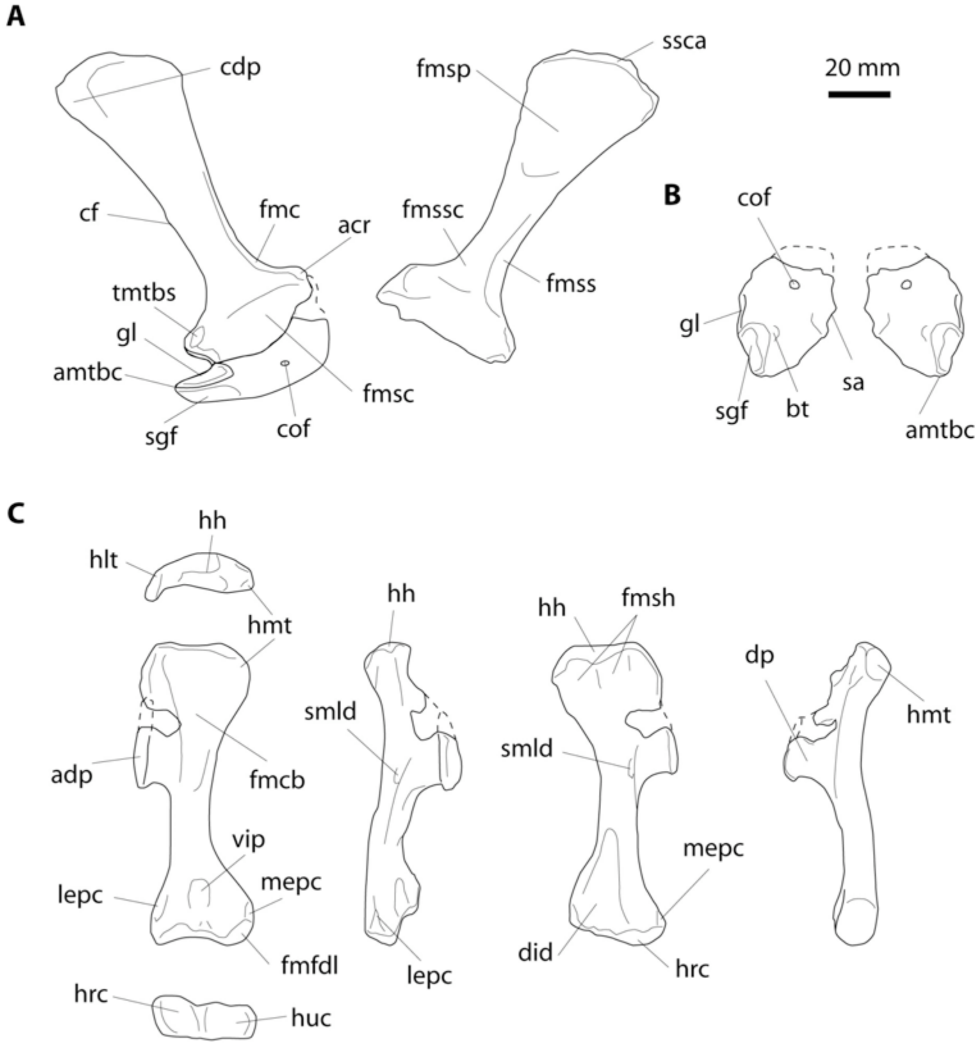

Figure 6-2. Osteological structures of the pectoral girdle and humerus of *Saturnalia,* based on MCP 3844-RV and 3845-RV. A, scapulocoracoid in lateral (left) and medial (right) views. B, coracoids in ventral view. C, humerus in (from left to right) proximal, ventral, distal, cranial, dorsal, and caudal views.

Humerus. As noted by Langer et al. (2007), a characteristic feature of the humerus of *Saturnalia* is the low grade of torsion between the proximal and distal ends, which is only about 10°. The proximal end is slightly more expanded than in other basal dinosaurs. The enlarged medial tuberosity shifted distally, and bulges caudomedially from the proximal expansion. It is not deflected towards the developmentally dorsal side of the shaft, as is the case in theropods. The proximal part of the deltopectoral crest is ventrally expanded, forming an oval fossa on its dorsocranial side. Distocaudally and slightly dorsally to that depression, a prominent, sharp ridge separates the cranial face of the deltopectoral crest and the dorsal side of the humeral shaft. This ridge extends distally to the base of the distal expansion. An oval rugosity is situated immediately caudodorsal to this crest (fig. 6-2). The apex of the considerably enlarged deltopectoral crest projects over its base cranially, caudally, and also distally. The distal base of the deltopectoral crest is short and oriented perpendicularly to the axis of the shaft. Distally on the ventral side of the humerus, an oval cavity is found in between and somewhat proximal to the distal condyles, like in *Eoraptor*. However, except of this cavity, the intercondylar fossa is not well developed. The form of the sharp, ridge-like epicondyles is decribed in detail by Langer et al. (2007). Intense striations are found dorsally on the distal expansion. The distocaudal corner of the humerus is enlarged and rugosely pitted.

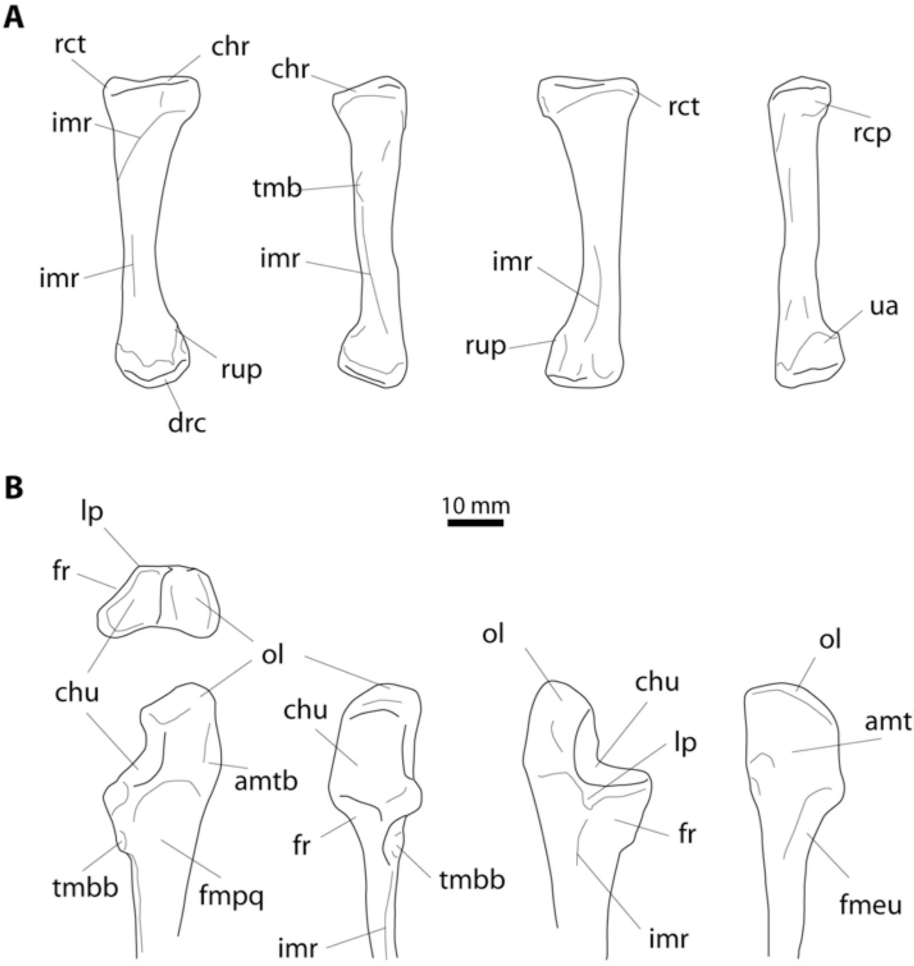

Figure 6-3. Osteological structures of radius (A) and ulna (B) of *Saturnalia*, MCP 3844-RV. From left to right, medial, cranial, lateral, and caudal views. A proximal view of the ulna is given above the medial view of this element.

Antebrachium. Radius and ulna are described in length by Langer et al. (2007), leaving not much to add. However, some of the structures are interpreted differently here in terms of muscular attachments (see below). The most peculiar modifications in comparison to other basal dinosaurs are an exceptionally large olecranon process of the ulna, an enlarged cranial tubercle on the proximal expansion of the same element, and an expanded facet for articulation with the ulna caudolaterally on the distal end of the radius (fig. 6-3). Like in other basal dinosaurs, a distinct tubercle ('biceps tubercle', see below and chapter 5) projects cranially, right distal to the proximal third of the radius. Moreover, a prominent caudal process projects proximally from the proximal articular surface of the radius. In general proportions, the radius of *Saturnalia* is significantly stouter and shorter with respect to the humerus than the same element of *Eoraptor*. The same was probably true for the ulna, which is incompletely preserved in *Saturnalia*.

Other basal sauropodomorphs

The following description of the forelimb anatomy of a basal sauropodomorph is primarily based on *Efraasia minor* (specimens SMNS 12354, 12667, and 17928). Comparisons with *Thecodontosaurus* (mainly YPM 2192) and *Pantydraco* are also included, but the taxonomy of these forms is debated (Benton et al., 2000; Yates, 2003a; Galton et al., 2007). The hypodigm of *Efraasia* (following Yates, 2003b) comprises some specimens with apparently deviant morphologies (SMNS 12668, 12684, the humerus of SMNS 17928). However, it is unclear in how far the extensive diagenetic deformation these elements exhibit may have affected their general characters. Similar shape might not reflect taxonomy in this case, but geological processes such as compression and folding. In addition, sexual dimorphism may also have played a role (Galton, 1997, 1999; Benton et al., 2000). Nevertheless, all these taxa have several osteological characters in common that are derived with respect to *Saturnalia* and other basal dinosaurs. These characters will be summarized below.

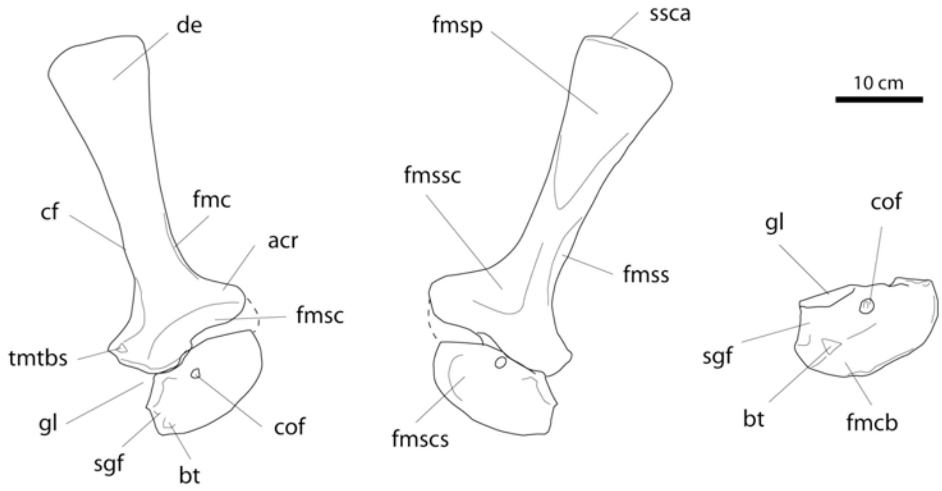

Figure 6-4. Osteological structures of the pectoral girdle of basal sauropodomorphs (here *Efraasia*, SMNS 12684 and 12667). Left, scapulocoracoid in lateral view, center, in medial view. Right, coracoid in ventral view.

Scapulocoracoid. The blade of the scapula is long and straight. It has a weak distal expansion (fig. 6-4) that is differentiated into two facets, the larger one occupying the cranial two thirds of the blade. A triangular caudodistal expansion as in *Saturnalia* is missing in *Efraasia*, but present in *Thecodontosaurus*. Another character of *Thecodontosaurus* that resembles *Saturnalia* is the dorsally vaulted distal edge of the scapular shaft. A faint caudal flange is found close to the base of the shaft in all basal sauropodomorphs. On the medial side of the blade behind this flange, there is an elongate, curved facet, which is bordered by a prominent ridge cranially. The distal half of the medial side of the scapular blade is flattened. A large, triangular depression extends proximocranially over the base of the blade and the scapular head. The distal rim of the shaft is slightly thickened medially, indicating the suprascapular attachment. Cranially on the lateral side, there is a craniocaudally narrow facet that extends over the proximal third of the shaft. The acromial region is dorsoventrally wide. A distinct tubercle or facet for articulation with the clavicle could not be identified. The angle between the acromion and the shaft is low, and there is no distinct acromial crest dorsal to the ventrolateral fossa (however, this seems to be subject to individual variation, or to the state of preservation: SMNS 12684 has a distinct acromial crest). The ventrolateral fossa is connected to the glenoid via a narrow channel. Compared to more basal dinosaurs, the scapular head is low in dorsoventral direction, but wide craniocaudally. Dorsal to the glenoid, the triceps tubercle projects caudolaterally, in some specimens laterally.

On the coracoid, the subglenoid fossa is reduced (fig. 6-4). Only a transversely concave but craniocaudally convex facet indicates the insertion of M. costocoracoideus. Immediately cranioventral to this facet, the triangular biceps tubercle is considerably enlarged. Cranioventrally to the biceps tubercle, there is a striated, oval depression. The caudoventral corner of the coracoid bears a strong, tuberculous process. The medial side of the coracoid is strongly concave; its cranial half exhibits a deep, oval depression.

The glenoid is characterized by equally sized scapular and coracoidal parts. The latter part is more caudally directed than in *Saturnalia* and other basal dinosaurs. However, a lateral component in the orientation of the articular surfaces is preserved. The glenoid opens caudoventrally with an angle of about 100°. Unlike *Saturnalia*, glenoid lips are faint or missing both on the coracoidal and the scapular part.

The scapulocoracoid articulation is complex and subject to variation. The lateral rim extends further ventrally than the medial rim, both enclosing a narrow groove close to the medial side of the suture. Moreover, there is a tuberculous swelling centrally on the medial base of that lateral rim. The coracoidal part of the suture bears a peg-like tubercle cranially that fits into a depression on the scapular part. Functionally, the scapulocoracoid articulation is a stabilizing joint and does not allow for independent movements, but permits some grade of flexibility between scapula and coracoid.

Humerus. The humerus of basal sauropodomorphs like *Efraasia* exhibits two main differences to *Saturnalia*. First, the medial tuberosity is considerably enlarged and somewhat distally shifted, forming a huge tubercle on the caudoproximal side of the shaft. Second, the distal expansion is twisted relative to the proximal end (fig. 6-5A). The original degree of torsion is hard to assess with the present material, since all humeri are deformed to a certain extent. However, in *Thecodontosaurus* (YPM 2195) the angle is about 45°. The straight apex of the cranioventrally directed deltopectoral crest is elongate, and extends over one fourth of the length of the humerus. Cranially on the dorsal side of the humerus, the lateral tubercle is prominent. The humeral head extends somewhat onto the dorsal side of the shaft. In some specimens of *Efraasia*, the dorsocranial ridge on the proximal humeral shaft is sharp and strongly developed; in others, it is missing. Like in *Saturnalia*, there is an oval scar adjacent to this ridge. On the distal end, the radial and ulnar condyles form a common articular surface ventrally, but are clearly separated dorsally. Also like in *Saturnalia,* a dorsal intercondylar depression and a ventral intercondylar pit are retained.

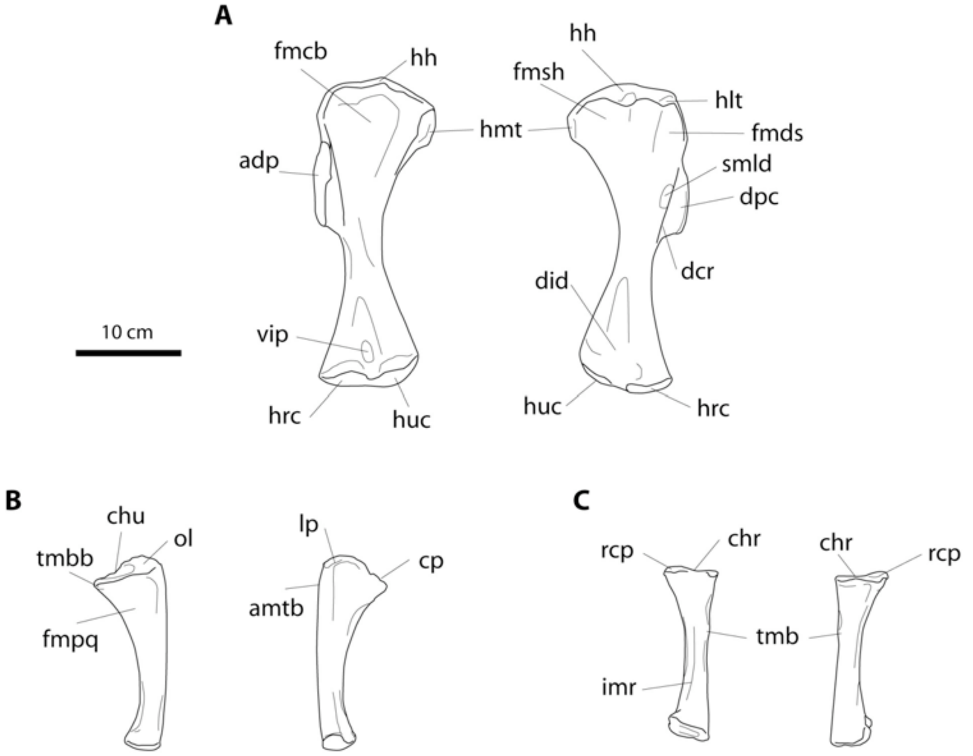

Figure 6-5. Osteological structures of the forelimb elements of *Efraasia* (SMNS 12354). A, humerus in ventral (left) and dorsal (right) views. B, ulna in medial (left) and lateral (right) views. C, radius in lateral (left) and medial (right) views.

As mentioned above, the form of basal sauropodomorph humeri is subject to considerable variation, probably at least in part due to diagenetic deformation. *Thecodontosaurus* (YPM 2195) and *Pantydraco* (BMNH P19/7; Galton et al., 2007) differ from *Efraasia* in the following characters: the humeral shaft is significantly more slender; the triangular medial tuberosity is more pointed; and the short deltopectoral crest extends only over about one third of the length of the humerus, leading to a shorter apex and a more triangular outline of the crest. However, considering the ongoing debate about the taxonomy of prosauropods from British Rhaetic fissure fillings (von Huene, 1908, 1914; Galton, 1973, 1985b, 1997, 1999; Kermack, 1984; Benton et al., 2000; Yates, 2003a; Galton et al., 2007), the significance of these observations remains unclear until articulated specimens will be discovered. Nevertheless, the *bauplan* of the humerus and configuration of muscular attachments in these forms is comparable to *Efraasia*.

Antebrachium. The radius of *Efraasia* (fig. 6-5B) is comparable to that of *Saturnalia*, both in relative size (compared to the humerus) and robustness. Differences include details in the configuration of the intermuscular ridges, and the form of the distal expansion. However, the latter part of the bone is deformed in *Efraasia*.

The ulna (fig. 6-5C) exhibits several differences. There is no ossified olecranon process; the caudal part of the proximal end of the bone exhibits a low, rounded swelling instead that may have served for the attachment of a cartilaginous extension, as indicated by a roughened, pitted surface. The shaft of the ulna appears to be more robust, but the whole element is transversely compressed. A proximocranial tubercle for the insertion of M. biceps brachii and M. brachialis is present, but is not as pronounced as in *Saturnalia*.

Manus. One specimen of *Efraasia* (SMNS 17928) preserves the complete metacarpus (however, metacarpals I and III are damaged), and also a number of phalanges. Elements of the carpus have not been reported for *Efraasia*, but are present in a fully preserved manus of *Thecodontosaurus* (YPM 2195). Since the hand of *Saturnalia* is not preserved, comparisons can only be made with *Eoraptor*, the closest outgroup relative.

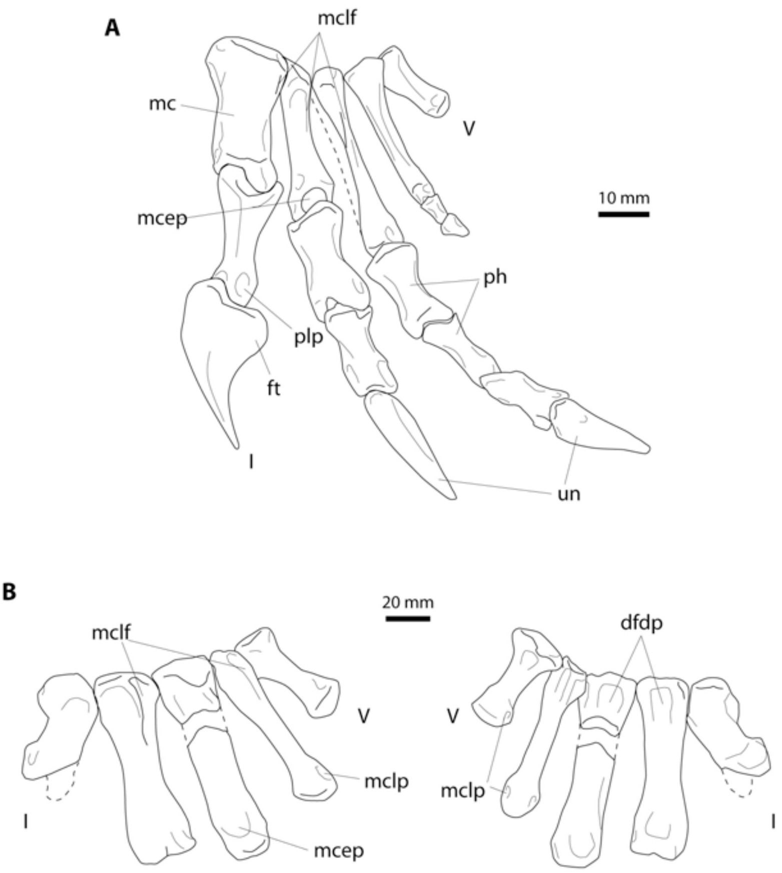

Figure 6-6. Reconstructions of the hand of *Thecodontosaurus* (A), and of the metacarpus of *Efraasia* (B; left, dorsal view; right, ventral view).

The metacarpus of *Efraasia* resembles *Eoraptor* in a number of characters. However, due to diagenetic deformation, there are not many details to observe. Metacarpal I is robust, but not considerably wider than metacarpals II and III (fig. 6-6B). Poorly defined extensor pits are present distally on the dorsal sides of metacarpals II and III. Proximolaterally on metacarpals II–IV, there are distinct flanges extending over the proximal quarter of the bone. Metacarpals IV and V are more slender than the preceding metacarpals. Their distal articular surfaces appear functional, but are not subdivided into lateral and medial condyles. Weak lateral ligament pits are present both on metacarpal IV and V. Metacarpal V is proximally wide and even longer than metacarpal I, but this may be due to shearing and the loss of the distolateral condyle in the first metacarpal.

The hand of the stratigraphically younger form *Thecodontosaurus* is better preserved, but exhibits a number of derived characters (fig. 6-6A). Benton et al. (2000) described three disc-like distal carpals capping metacarpals I-III, like in *Eoraptor* (chapter 5). Metacarpal I is much more robustly developed than the remaining metacarpals. In proximal view, the articular surface is subtriangular with a rounded medial corner. Like in all basal dinosaurs, the distal condyles are asymmetrical, with the lateral condyle being larger, laterally inclined, and extending further distally, while the medial condyle extends far proximally on the ventral side. Metacarpal II is a rod-like bone and has a triangular proximal articular surface, with a slight flange that extends dorsolaterally. Distally, the dorsal surface of metacarpal II bears a large, well-defined extensor pit, and an oval ligament pit laterally. Metacarpal III is more slender than metacarpal II. An extensor pit is present on the distal expansion, but less distinctly developed than in metacarpal II. There is no clear ligament pit laterally; the medial side cannot be examined. Metacarpal IV is similar to metacarpal III in general shape. Its distal expansion is dorsoventrally compressed and exhibits no extensor or ligament pits. The distal condyles are reduced to small, semispherical knobs. Metacarpal V is short and robust, and has a flattened distal surface that shows no traces of articular condyles. In proximal view, the metacarpus is slightly arched, but due to deformation the original angle cannot be reconstructed reliably.

The phalangeal formula of *Thecodontosaurus* is 2-3-4-2-0. Digit I comprises an elongate proximal phalanx with a distinct ligament pit laterally (but not medially), and a short, deep but transversely narrow ungual. The latter element has a strong curvature, and bears a large flexor tubercle ventrally. The unguals of digiti II and III are smaller, but similarly shaped. The phalanges of digiti II and III are shorter and more robustly developed than phalanx I.1, and exhibit a slight asymmetry with a lateral distal condylus that is laterally flared. Two phalanges are retained in digit IV, but these are strongly reduced. There are no phalanges articulating with metacarpal V.

Muscle reconstructions

Referring to the discussion on phylogenetic inferences of archosaurian forelimb musculature (chapter 3), and in comparison with the results of chapters 4 and 5, attachment sites of the forelimb muscles in basal sauropodomorphs are reconstructed in figs. 6-7 to 6-10.

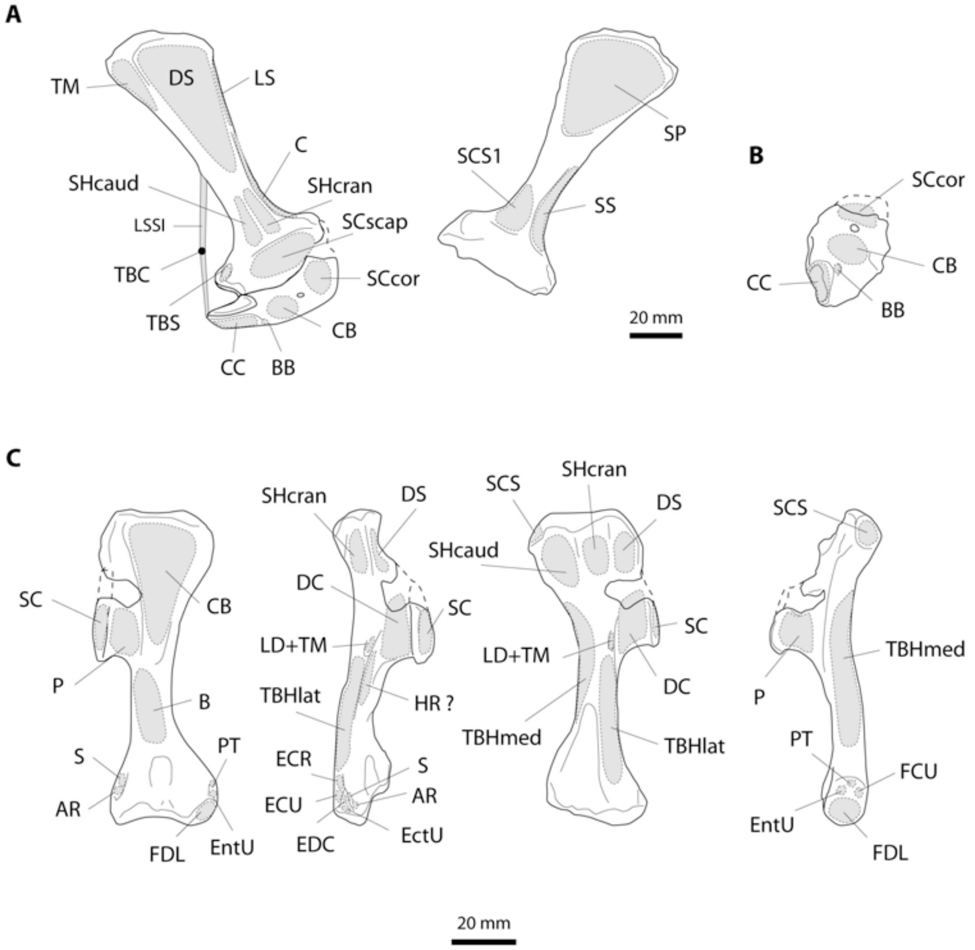

Figure 6-7. Reconstructions of the muscular attachments on the scapulocoracoid (A) and humerus (B) of *Saturnalia*. A, scapulocoracoid in lateral (left) and medial views. B, coracoid in ventral view. C, from left to right: humerus in ventral, cranial, dorsal, and caudal views. For explanations see text.

Saturnalia

Generally, the shoulder girdle musculature of *Saturnalia* as inferred here is comparable to that of *Lewisuchus* and *Eoraptor*. Cranioproximally on the scapular blade, the facet for M. cucullaris is not caudally expanded as in *Eoraptor* (however, this feature of *Eoraptor* may also be an artefact, see chapter 5). The main differences in *Saturnalia* are: the type of differentiation of the scapular blade, which provides only little room for the origin of a M. teres major on the caudodistal process; and the restriction of the fossa for the origin of M. subscapularis to the cranial part of the base of the scapular blade (fig. 6-7A). The latter modification may also be the cause for the craniocaudal constriction of the proximal scapular blade (see chapter 5, *Herrerasaurus*). Moreover, the different shape of the subglenoid fossa may indicate an altered angle of insertion or a weaker development of M. costocoracoideus. The relatively small biceps tubercle has shifted cranially relative to the glenoid, slightly more so than in basal theropods (chapter 5). The remaining muscles exhibit a configuration that is very similar to that of *Lewisuchus, Eoraptor*, and basal theropods.

The humerus of *Saturnalia* exhibits major modifications of the plesiomorphic condition. The elongate apex of the deltopectoral crest might indicate a stronger development of M. supracoracoideus. An enlargement of the sites of insertions of M. pectoralis and M. deltoideus clavicularis might also have triggered this size increase. On the developmentally dorsal side of the humerus, the additional fossa on the expanded proximal part of the deltopectoral crest may have served for an enlarged, fleshy attachment of M. deltoideus scapularis. Most notably, the scar for the insertion of M. latissimus dorsi and M. teres major shifted ventrocranially, being situated adjacent to the insertion of M. deltoideus clavicularis and the possible origin of M. humeroradialis (fig. 6-7). Since the tendon of M. latissimus dorsi plesiomorphically runs between Mm. triceps brachii capiti humerale laterale and mediale, this shift also caused a reconfiguration of these two muscles: The inferred site of origin of the medial head is enlarged and almost entirely occupies the caudal and caudodorsal sides of the shaft, while the origin of the lateral head is restricted to the distal half of the cranial side of the shaft. The form of the epicondyles resembles other basal dinosaurs, but the exact configuration of the attaching muscles cannot be inferred and is therefore a matter of speculation. However, because of the confined area of the epicondyles, alternative configurations of the origins of the epicondylar muscles do not have much effect on the reconstructed courses of the lines of action (fig. 6-11). Like in theropod dinosaurs, the distocaudal facet adjacent to the ulnar condyle is possibly related to an enlarged origin of M. flexor digitorum longus (also suggested by Langer et al., 2007).

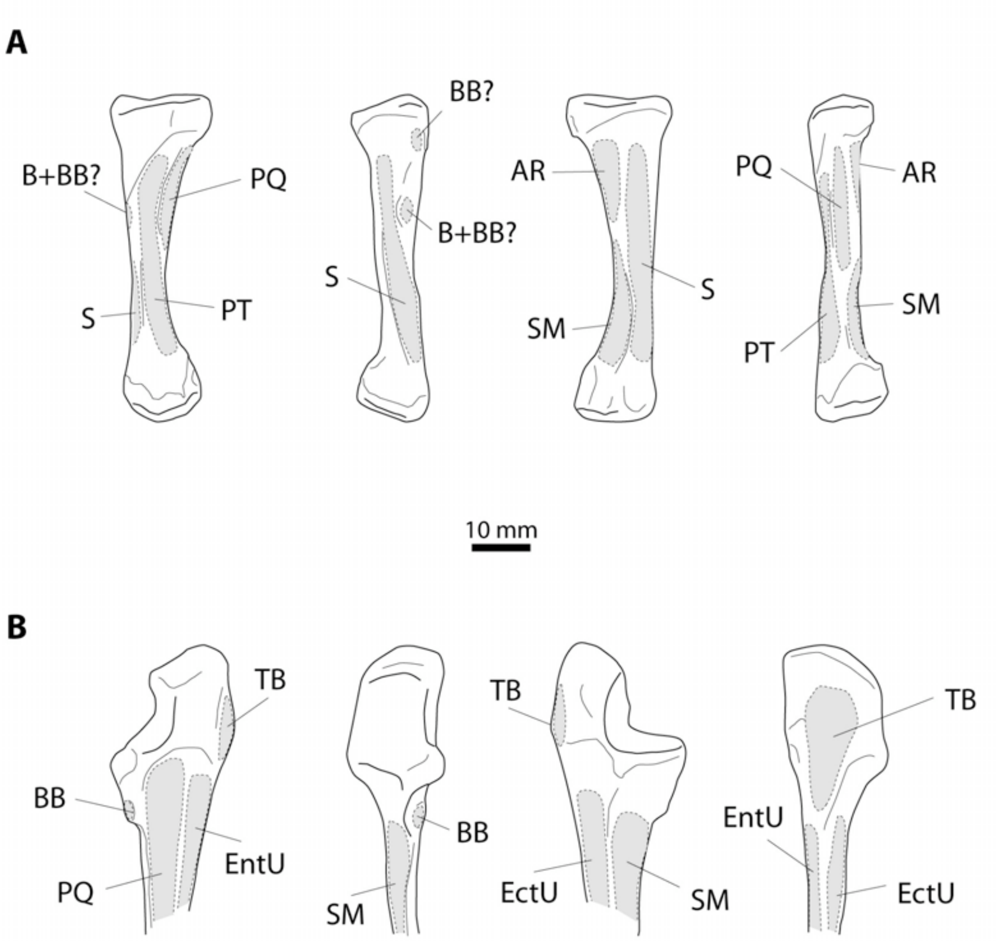

Figure 6-8. Reconstruction of the muscular attachments on the antebrachium of *Saturnalia*. A, radius; B, ulna. From left to right, medial, cranial, lateral, and caudal views. For explanations see text.

On radius and ulna of *Saturnalia,* no myological novelties could be recognized. With the exception of some proportional differences, the inferred muscle attachment sites are virtually identical to those of *Eoraptor* (fig. 6-8; see also chapter 5, fig. 5-16). The large olecranon process provides an extended area of insertion of M. triceps brachii, but the main purpose of this process probably was to serve as a lever (see Discussion below). The position of the cranial radial tubercle, which probably served for the insertion of M. brachialis (and possibly M. biceps brachii; see chapter 5, Discussion), is identical to *Herrerasaurus* and basal theropods. Since there is no trace of a proximal lateral tubercle on the radius, M. humeroradialis may have been reduced or lost. However, distal to the deltopectoral crest a possible site of origin of this muscle is preserved in *Saturnalia* (fig. 6-7).

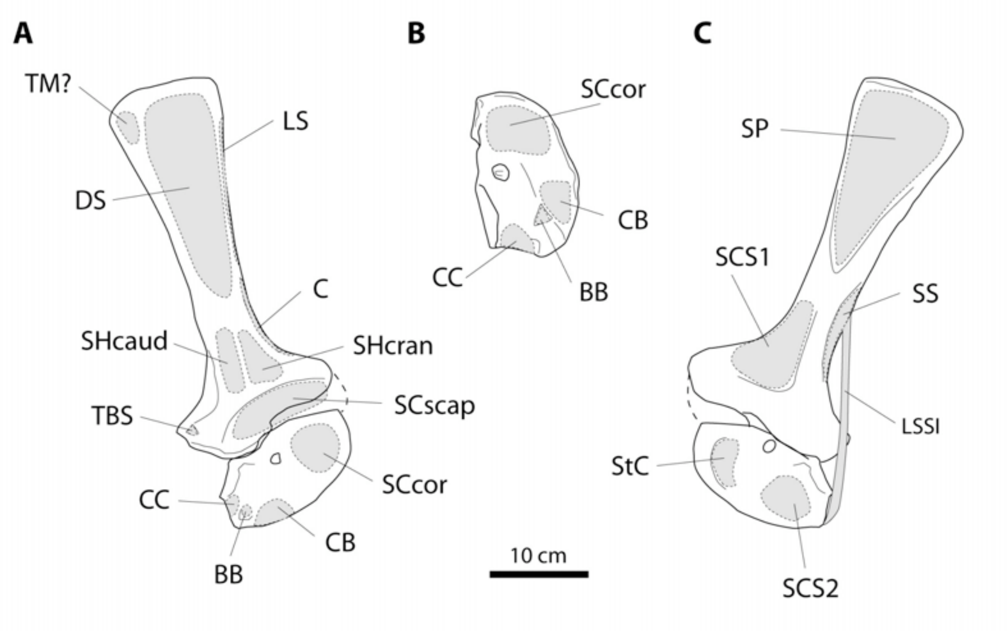

Figure 6-9. Reconstruction of the muscular attachments on the scapulocoracoid of *Efraasia*. From left to right: scapulocoracoid in lateral view; coracoid in ventral view; scapulocoracoid in medial view. For explanations see text.

Efraasia

The inferred muscle attachments sites on the pectoral girdle of *Efraasia* closely resemble those of *Saturnalia*. The evolutionary novelties observed in the latter taxon are also present in the former: the attachment of M. costocoracoideus is even less clearly defined, and the fossa for the origin of M. subscapularis, situated cranially on the medial side of the scapular head and of the base of the blade, is slightly enlarged relative to the size of the scapular head (fig. 6-9). Unlike *Saturnalia*, the origin of M. biceps brachii on the considerably enlarged coracoidal biceps tubercle has not shifted cranially, but remains in a position comparable to *Eoraptor* and basal theropods (chapter 5). The striated depression medial to the biceps tubercle probably indicates the origin of M. coracobrachialis, which is more medially located than in other basal dinosaurs.

The humerus of *Efraasia* is characterized by the osteological novelty of a twisted distal expansion, but this does not significantly affect the inferred sites of muscle attachment. In fact, the configuration of muscles is almost identical to *Saturnalia*, with the exception of a more proximally (but still cranially) placed insertion of M. latissimus dorsi and M. teres major. In addtition, the insertion of M. subscapularis shifted caudodistally, due to the enlargement of the medial tuberosity (fig. 6-10A). The enlarged cranioproximal fossa on the dorsal side of the humerus may relate to a size increase of M. deltoideus scapularis, which in turn may explain the enlargement and elongation of the scapular blade (the origin of this muscle) relative to the scapular head (see fig. 6-9).

Like in *Saturnalia*, the inferred muscle attachment sites on radius and ulna are conservative (fig. 6-10B+C) in *Efraasia*. The seemingly enlarged fossa for the origin of M. pronator quadratus on the medial side of the ulna may indicate an increased size of this muscle, but this inference is rather speculative considering the high grade of distortion of this element.

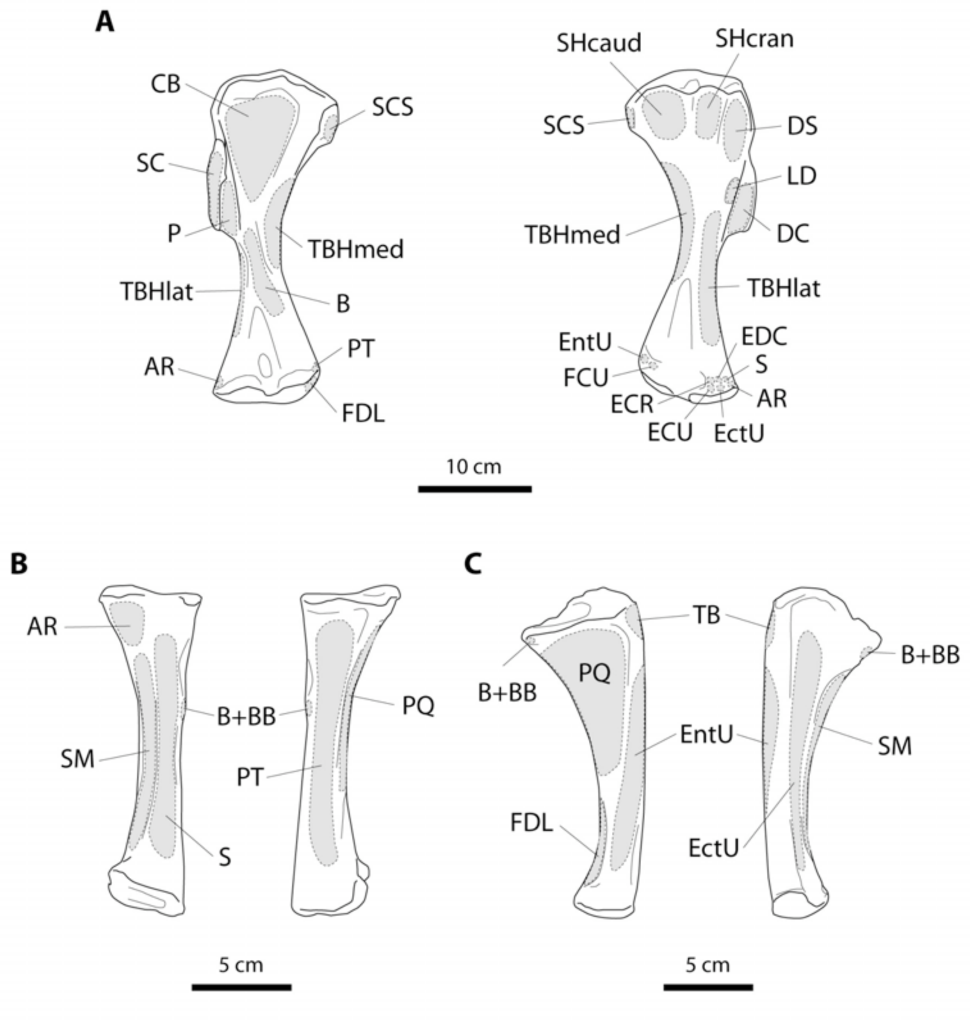

Figure 6-10. Reconstruction of muscle attachment sites on the humerus and antebrachium of *Efraasia*. A, humerus in ventral (left) and dorsal (right) views. B, radius in lateral (left) and medial (right) views. C, ulna in medial (left) and lateral (right) views. For explanations see text.

Discussion

The morphological differences between basal sauropodomorphs and other basal dinosaurs pertain primarily to the humerus and the musculature that acts on it, while the cingulo-axial muscles retain a conservative configuration (fig. 6-12). The craniocaudally wide humeral head, combined with an elongate, caudolaterally directed coracoidal part of the glenoid, permitted protraction and retraction only when the humerus was abducted by about 20° or more, as has been demonstrated by Langer et al. (2007). The presence of a distinct ventral intercondylar pit probably indicates that the forelimb was used to support the body in a semi-erect stance with a flexed elbow joint, like in *Eoraptor* (see chapter 5).

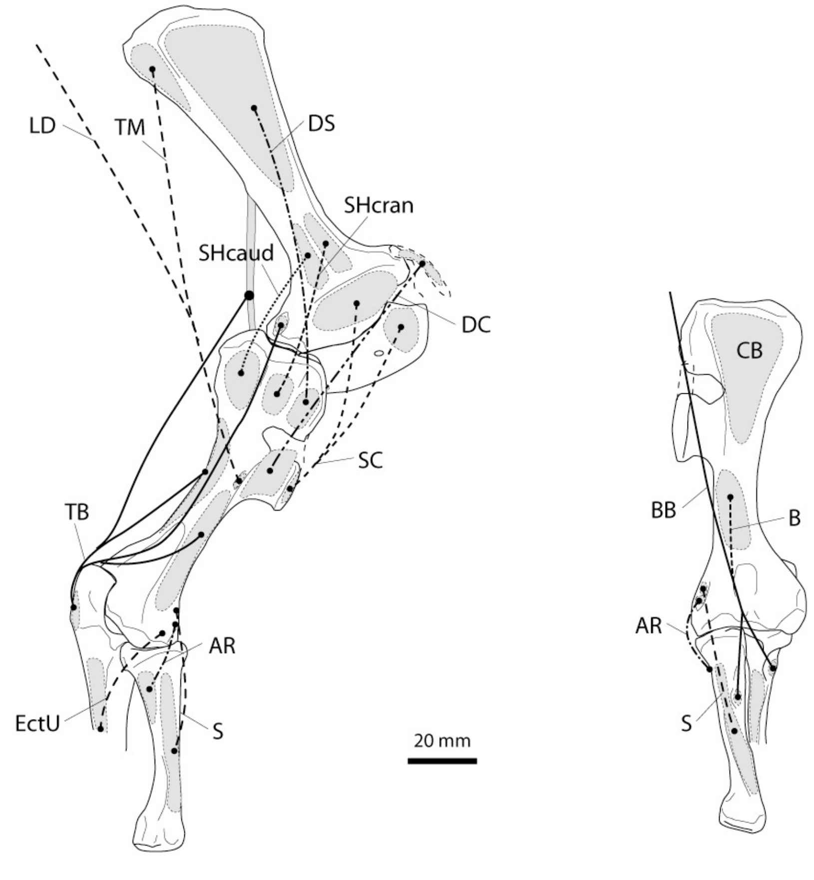

Figure 6-11. Reconstruction of the skeletomuscular system of the shoulder girdle and forelimb of *Saturnalia*. Left, scapulocoracoid and forelimb in lateral view. Right, humerus and antebrachium in ventromedial view. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle.

As a result of the enlargement of the deltopectoral crest, the insertion areas of the deltoid and pectoral muscles increased, which possibly indicates an increase in relative size of these muscles. Moreover, because of the elongation of the deltopectoral crest, the insertions of M. pectoralis, M. deltoideus clavicularis, and M. supracoracoideus shifted distally (figs. 6-11, 6-13). Probably, the consequence was an increase in force (accompanied by a reduction of speed) during protraction and retraction, following the classic laws of leverage (see Gregory, 1912; Hildebrand and Goslow, 2001). The sigmoid form of the humerus of basal sauropodomorphs (see also chapter 7) might relate to this issue, since such a shape is assumed to be optimal for a compact configuration of voluminous muscles (Lanyon, 1980, 1981; Cubo et al., 1999). More powerful protractors and retractors may have been crucial for size increase in basal sauropodomorphs, if the semi-erect posture of the humerus is retained and the forelimb is used for locomotion (Biewener, 1989a,b, 1990). However, since the same modifications are found not only in large sauropodomorphs like *Efraasia* but also in *Saturnalia* (a taxon not significantly larger than *Eoraptor*), there was probably a second evolutionary factor behind these adaptations.

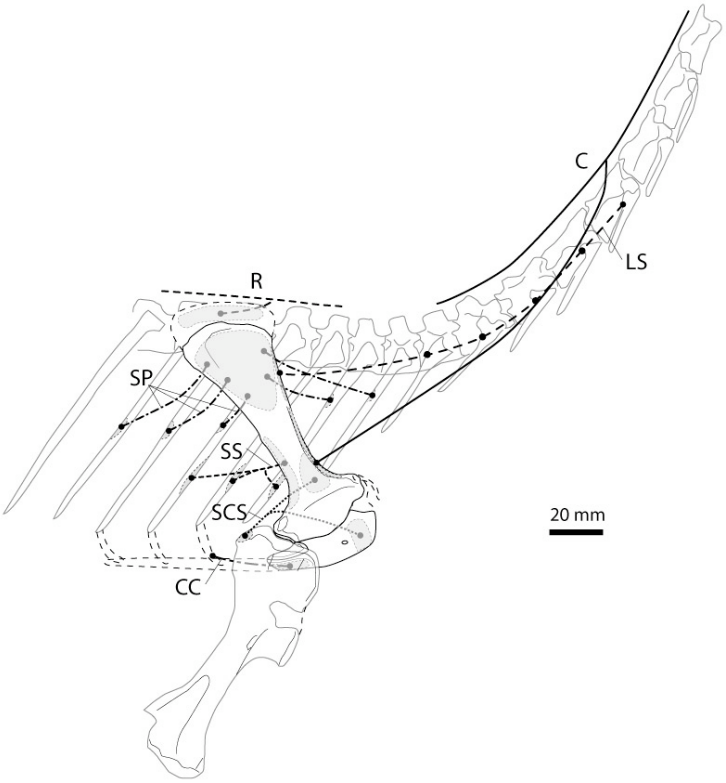

Figure 6-12. Reconstruction of the cingulo-axial skeletomuscular system and Mm. subcoracoscapulares in *Saturnalia* (lateral view). Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle. Shaded areas and lines of action indicate that the muscle lies on the remote side of the bone.

The most significant modifications of the sauropodomorph myology compared to other basal dinosaurs are found in the courses of M. latissimus dorsi / M. teres major and M. subscapularis (figs. 6-11, 6-12, 6-13). The cranial shift of the insertion of M. latissimus dorsi and M. teres major added a rotational component to the movement of the humerus during retraction, leading to supination of the hand. This effect is enforced by the outward twist of the distal expansion of the humerus relative to the proximal end. The cranioventral shift of the origin of M. subscapularis likewise made the humerus to rotate outwardly around its long axis during contraction of this muscle, replacing the plesiomorphic retractive-adductive movement. The possibly enlarged M. deltoideus scapularis might have assisted in this action, since it had its origin caudodorsal and its insertion cranial to the pivot in the glenoid joint. It is to note that a strong rotation during retraction of the humerus would probably have been avoided if only M. pectoralis contracted. Therefore, the skeletomuscular system of the sauropodomorph forelimb appears to be adapted for supinating the manus during retraction of the humerus, but it is probable that the animal could control the grade of supination by means of differently contracting the muscles that are involved in this system. The significance of these adaptations is not entirely clear, but the ability to control the orientation of the palm may have been advantageous for grasping (see below).

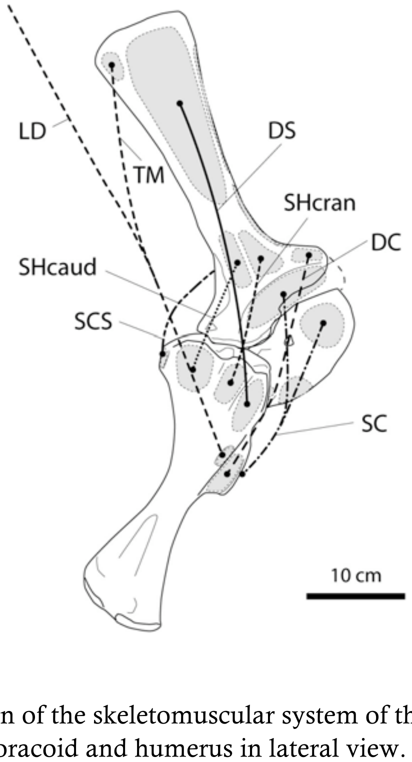

Figure 6-11. Reconstruction of the skeletomuscular system of the shoulder girdle of *Efraasia*, showing scapulocoracoid and humerus in lateral view. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle.

The conservative anatomy of the antebrachium exhibits no other specializations in this regard. Like in *Eoraptor*, the position of the cranial tubercle of the radius (the site of insertion of M. brachialis, M. biceps brachii, or both) supported pronation of the manus when the elbow joint was flexed (fig. 6-11). In *Efraasia,* the enlarged biceps tubercle on the coracoid may correlate to a more powerfully developed M. biceps brachii. On the one hand, this may be correlated to the size increase of these animals, which made a positively allometric growth of the musculature necessary (Biewener, 1989a,b, 1990). On the other hand, the presence of a large olecranon in *Saturnalia* may relate to grasping improvements, since this process works as a lever to transfer forces exerted by M. triceps brachii to the distal part of the ulna. Hence, a proximally extended olecranon process enabled a more powerful extension of the antebrachium (fig. 6-11). If M. triceps brachii were enlarged for these reasons, a powerful antagonist (M. biceps brachii) would have been a consequence.

Finally, the enlargement and strong asymmetry of the first digit of the hand, accompanied by the elongation of the phalanges in digits II and III, indicates increased grasping abilities at least in forms like *Thecodontosaurus.* The evolution of grasping abilities in basal sauropodomorphs was corroborated by the development of large flexor tubercles on the unguals, and by the size increase of the distocaudal humeral facet, which possibly correlates to the origin of M. flexor digitorum longus. The enlargement of this facet parallels similar modifications in theropods (chapter 5).

Conclusions

Both osteology and inferred myology indicate that basal sauropodomorphs lacked adaptations for an improved mode of locomotion in the forelimb. If used for quadrupedal locomotion, a slow, semi-sprawling gate (as inferred for *Eoraptor*, see chapter 5) would have been the consequence. On the other hand, the first known sauropodomorphs already exhibit a number of adaptations for grasping. In contrast to theropods, the skeletomuscular system of the shoulder region is optimized for increased power and control of such a movement, but not for velocity. Therefore, the muscle reconstructions presented here confirm that prosauropods were able to powerfully manipulate branches and other plant parts with their hands, as has been suggested previously (see review by Galton and Upchurch, 2004). Nevertheless, the osteological and myological features of these forms are still generalized enough to permit multiple uses of the pectoral extremity, including locomotion.

7 'Prosauropod' forelimb anatomy and the transition to Sauropoda

Introduction

Non-sauropod sauropodomorphs, commonly summarized as 'prosauropods', are a distinct group of dinosaurs that persisted for about 50 million years, from the Carnian possibly up to the Bajocian (fig. 7-1). However, the anatomy of these animals is rather uniform, leading to considerable uncertainty about their taxonomy and phylogenetic relationships. Recent phylogenetic analyses agree that *Plateosauravus* (formerly part of the hypodigm of '*Euskelosaurus*'; see van Heerden, 1979; Yates, 2003c) is one of the earliest and most plesiomorphic members of this group, aside from *Saturnalia* and *Efraasia* (Upchurch et al., 2007; Yates, 2007). Moreover, there is a consens that *Melanorosaurus* and *Antetonitrus* stand close to (or actually are, depending on the taxonomic nomenclature used) the first sauropods (Yates and Kitching, 2003; Yates, 2004; Upchurch et al., 2007; Yates, 2007). However, the relationships of the remaining non-sauropod sauropodomorphs are strongly debated. In addition to the discussion about the existence of monophyletic 'core'-Prosauropoda (chapter 1), the positions of individual OTUs are also highly variable in published topologies. For example, *Lufengosaurus* has been regarded as closely related to *Plateosaurus* (Galton and Upchurch, 2004), as outgroup to Plateosauridae (Upchurch et al., 2007), or as a sister-taxon to *Massospondylus* within a monophyletic Massospondylidae (Yates and Kitching, 2003; Yates, 2004; Yates, 2007). *Riojasaurus* grouped together with *Melanorosaurus* and *Lessemsaurus* (Galton and Upchurch, 2004), with *Plateosaurus* and *Coloradisaurus* (Upchurch et al., 2007), as the basal-most member of the 'core'-Prosauropoda that include the latter two taxa and *Massospondylus* + *Lufengosaurus* (Yates and Kitching, 2003; Yates 2004), or as the sister-taxon to Massospondylidae + more derived sauropodomorphs (Yates, 2007). Similar examples could also be given for other 'prosauropod' taxa. Considering that the published topologies – when compared – almost appear to constitute random shuffling of 'prosauropod' OTUs, there is currently no consensus in sight. In future, a better understanding of basal sauropodomorph interrelationships will hopefully be possible by means of highly detailed phylogenetic analyses (Rauhut et al., in prep.), and by new finds especially from the Carnian, the geological age when most cladogenetic events within this group probably took place (fig. 7-1). In this work, the phylogenetic hypothesis of

Yates (2007) is chosen as a framework, because it is based on a matrix that currently scores the highest number of characters (348), and most closely reflects a trend in modifications of the functional morphology of the forelimb towards sauropod conditions (see below, chapter 9). However, the anatomical observations presented here possibly will have to be re-evaluated once a consensus on basal sauropodomorph phylogeny is established.

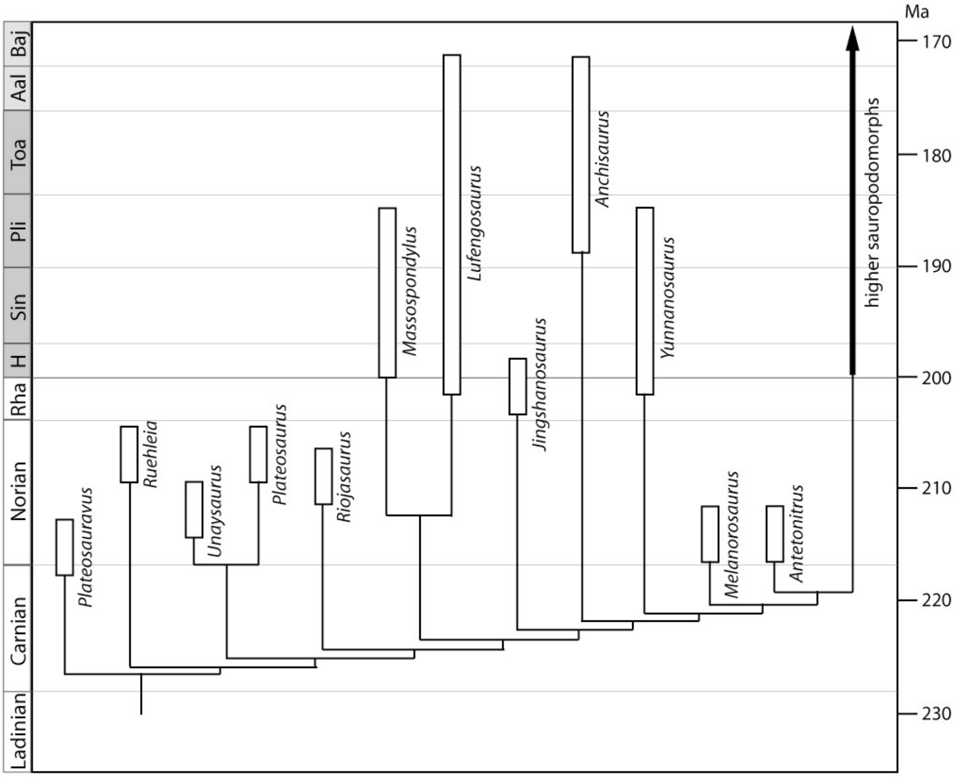

Figure 7-1. Phylogenetic relationships and temporal distribution of the taxa discussed in this chapter. Cladogram based on Yates (2007).

The forelimb of most non-sauropod sauropodomorphs exhibits only minor modifications with respect to the basal-most members of this clade (see chapter 6). Naturally, this uniformity hampers the recognition of evolutionary trends. However, there are some specializations, and a number of large forms show changes that may represent the first steps toward sauropod forelimb anatomy. Based on the specimens listed in chapter 2, this chapter intends to present the variety of 'prosauropod' forelimbs, and to discuss functional interpretations. Moreover, the forelimb anatomy of the sauropodomorph most closely related to true sauropods, *Antetonitrus ingenipes*, will be described and discussed in detail. This taxon represents the starting point for major modifications of the forelimb skeletomuscular system in more derived sauropods (see chapters 8, 9).

Anatomy

Galton (1990) and Galton and Upchurch (2004) reviewed the forelimb anatomy of basal sauropodomorphs. However, these works generalize some important intergeneric differences that may be important for the understanding of sauropodomorph forelimb evolution (chapter 9), making an own review on ‘prosauropod’ forelimb anatomy necessary. More detailed descriptions of the forelimb osteology of individual taxa have been published for *Anchisaurus* (von Huene, 1906, 1914; Lull, 1953), *Jingshanosaurus* (Zhang and Yang, 1995), *Lufengosaurus* (Young, 1941), *Massospondylus* (Broom, 1911; Cooper, 1981), *Melanorosaurus* (Bonnan and Yates, 2007), *Plateosaurus* (von Huene, 1926), *Riojasaurus* (Bonaparte, 1969, 1971), *Unaysaurus* (Leal et al., 2004), and *Yunnanosaurus* (Young, 1942).

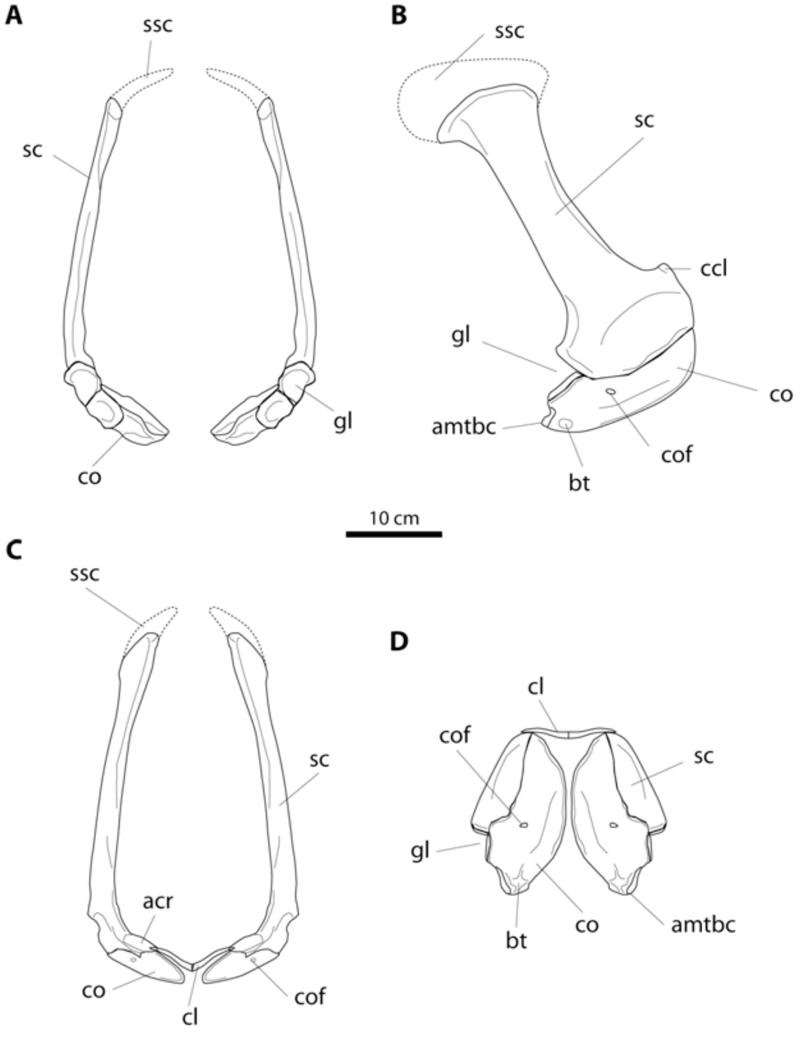

Figure 7-2. Three-dimensional reconstruction of the pectoral girdle in *Massospondylus*, based on the articulated specimen BP/1/5241, which also preserves clavicles. A, caudal view; B, lateral view; C, cranial view; D, ventral view.

Non-sauropod sauropodomorphs

***Bauplan* of the pectoral girdle.** Our understanding of the structure of the pectoral girdle in basal sauropodomorphs has recently been much improved by the discovery of exquisitely preserved, fully articulated specimens of *Massospondylus* (Yates and Vasconcelos, 2005). The shoulder girdle elements of these finds are almost undeformed and have a largely intact surface. Moreover, for the first time in sauropodomorphs, clavicles are found in articulation with the scapula. The paired clavicles articulate in midline, forming a wide, V-like brace that closely resembles the furcula of theropods (Yates and Vasconcelos, 2005). Disarticulated, but similarly shaped clavicles have also been reported for *Plateosaurus* (von Huene, 1926).

With the width of the clavicles and their point of articulation on the scapula as constraints, the shoulder girdle of *Massospondylus* can reliably be reconstructed in three dimensions (fig. 7-2). It becomes evident that the plesiomorphic *bauplan* of archosaurs (as observed in *Euparkeria*, see chapter 4) was retained in a number of aspects: the coracoids almost contact in midline; they are more ventrally than laterally oriented; the sternum must have been positioned caudal to the coracoids, not medially between them; and due to the orientation of the coracoids, the glenoid orientation has a major lateral component. In cranial view, the pectoral girdle of *Massospondylus* is deep and narrow, but widens caudally. Taking the room for Mm. serrati and M. subscapularis into consideration, the narrowly constructed pectoral girdle fits onto the ribcage only relatively far cranially placed, with the coracoids positioned ventral to the last cervical vertebra and the cervicodorsal transition. Since the structure of the scapulocoracoid is similar in all other basal dinosaurs and sauropodomorphs, such a construction probably applies also to these groups (see Discussion below, chapter 9).

Scapulocoracoid. The scapulae of most ‘prosauropods’ are very similar to the scapula of *Efraasia*. The blade is long and slender, and distally only moderately expanded. The scapular head is craniocaudally wide but dorsoventrally low. Differences exist in the relative position and size of the caudal flange of the scapular blade, in the relative size of the articular facet for the clavicles, in the grade of convexity of the distal edge of the blade, and in the form of the caudodistal process of the blade (fig. 7-3). In comparison to *Efraasia*, the cranial fossa for the insertion of M. cucullaris is smaller and more distally placed in most taxa except *Lufengosaurus*. A significant modification is seen in the angle between the cranial edge of the scapular blade and the dorsal rim of the acromion: This angle is plesiomorphically low (around 140°), but becomes smaller in *Massospondylus* and *Lufengosaurus* (around 100°). Uniquely in *Unaysaurus*, the fossa for the origin of M. supracoracoideus is restricted to the caudal half of scapular head, extending cranially only up to the 'kink' in the scapulocoracoidal suture (fig. 7-3). *Yunnanosaurus* has a scapular blade that is broadened relative to the scapular head, and lacks the facet for M. serratus superficialis medial to the caudal flange on the caudomedial side of the blade.

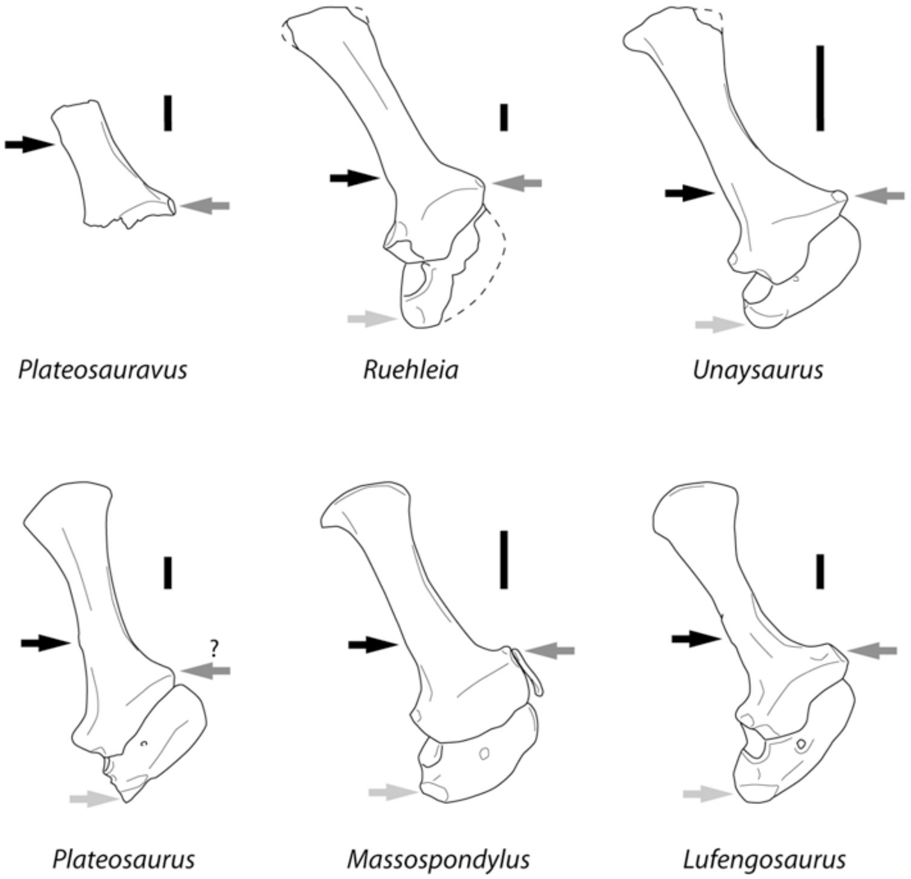

Figure 7-3. Comparison of scapulocoracoids of several 'prosauropods'. Black arrows indicate the caudal flange of the scapular shaft; medium grey arrows indicate the facet for clavicular articulation; light grey arrows indicate the tubercle for the origin of M. biceps brachii. Scale bar = 50 mm.

Regarding the coracoid, basal sauropodomorphs primarily differ in the relative size of the tubercle for the origin of M. biceps brachii. In many cases, a correlation to the size of the animal can be observed: the biceps tubercle is small in *Massospondylus,* but very large in forms like *Lufengosaurus* and *Yunnanosaurus*, where it even surpasses the size of the glenoid (fig. 7-3). The glenoid usually opens with a wide angle and is caudolaterally oriented. However, in *Plateosaurus* the angle is narrower and the orientation strictly caudoventral, with the coracoid contributing only little to the articular facet (fig. 7-3). Moreover, *Plateosaurus*, *Riojasaurus, Coloradisaurus, Lufengosaurus,* and *Massospondylus* exhibit a distinct subglenoid fossa, resembling the condition found in basal dinosaurs (see chapters 4 and 5). In other 'prosauropods', this area is saddle-shaped.

Sternal plates. Ossified sternal plates are known from a number of basal sauropodomorphs. Since articulated specimens of *Efraasia* (SMNS 12667) and *Thecodontosaurus* (YPM 2195) lack ossified sterna, their presence in *Plateosaurus* (von Huene, 1926), *Lufengosaurus* (Young, 1941), *Massospondylus* (Cooper, 1981), *Jingshanosaurus* (Zhang and Yang, 1995), and *Yunnanosaurus* (Young, 1942) possibly is a shared derived character. In most of these forms, the sternal plates have a suboval shape with a thickened, rugose craniolateral corner that serves for articulation with the coracoid. In *Massospondylus* specimen BP/1/4934, the sternal plates are lozenge-shaped and co-ossified (fig. 7-4). The presence of a longitudinal ridge on the ventral side of the sternum has been reported for *Massospondylus* (Cooper, 1981), *Lufengosaurus* (Young, 1941), and *Jingshanosaurus* (Zhang and Yang, 1995).

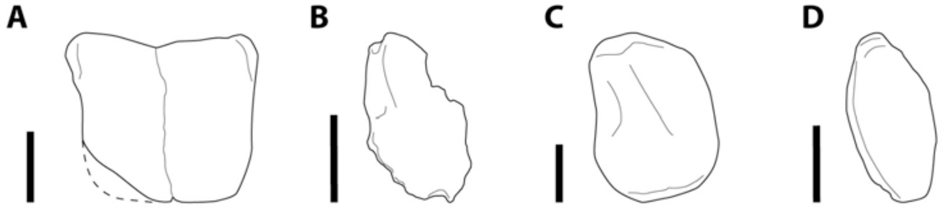

Figure 7-4. Comparison of 'prosauropod' sternal plates. A, co-ossified sternal plates of *Massospondylus* (BP/1/4934) in dorsal view. B, right sternal plate of *Massospondylus* (NMZ QG1159) in ventral view; after Cooper (1981). C, right sternal plate of *Lufengosaurus* (IVPP V15) in ventral view. D, ?right sternal plate of *Yunnanosaurus* (IVPP V20) in ventral view; after Young (1942). Scale bar = 50 mm.

Humerus. In non-sauropod sauropodomorphs, the shape of the humerus varies considerably, from relatively slender (*Plateosaurus*) to extremely robust (*Yunnanosaurus*). The embryonic form *Mussaurus* has very slender, elongate humeri that are not easy to compare to those of adult 'prosauropods' (Bonaparte and Vince, 1979). However, in general features adult 'prosauropod' humeri exhibit strong similarities to *Efraasia* (figs. 7-5, 6-5). Shared characters include a strongly concave curvature of the caudal side of the shaft; a slightly sigmoid outline in cranial view; an enlarged medial tuberosity of the humerus that is placed distal to the humeral head; a large deltopecotral crest that extends over 40-50% of the humeral length and is deeper than the humeral shaft is wide; a large distal expansion that equals the width of the proximal expansion (without the medial tuberosity); the presence of a ventral intercondylar depression that is, in most cases, not as deep and sharply delimited as in the basal-most sauropodomorphs (see chapter 6); and the presence of a dorsal intercondylar depression that is albeit weakly developed. The position of the scar for the insertion of M. latissimus dorsi and M. teres major is also conservative, but this character could only be found in *Plateosauravus*, *Unaysaurus*, and *Massospondylus*. Young (1947) reported a similar structure in *Lufengosaurus magnus* (IVPP V82). The morphological details of the deltopectoral crest (form in cranial view, angle of the apex relative to the shaft axis, angles of the proximal and distal bases relative to the shaft) vary considerably, rendering its form possibly diagnostic on the genus level.

Distinct modifications of the plesiomorphic state can be observed in the form of the proximal and distal articular ends (fig. 7-5). The plesiomorphic form of the proximal end is a slightly curved, ventrally concave bar, as seen in *Saturnalia, Efraasia* and *Plateosauravus*. In more derived sauropodomorphs, the humeral head becomes wider in dorsoventral and more compressed in craniocaudal direction, in combination with a vaulted outline of the proximal expansion in ventral and dorsal views (e.g., *Massospondylus*, *Lufengosaurus*, *Yunnanosaurus*). In addition, the medial tuberosity is caudodorsally angled with respect to the main axis of the humeral head. This angle is very low in *Unaysaurus* and *Massospondylus*, but distinct in *Lufengosaurus* and an unnamed taxon from the Argentinian Los Colorados Formation (PVL field number 6; fig. 7-5). Moreover, there are differences in the orientation of the deltopectoral crest: it is primarily ventrally oriented in *Plateosaurus*, but strongly cranioventrally deflected in *Massospondylus* and a number of other forms. However, the large sample of 'prosauropod' humeri from the Löwenstein Formation of southern Germany suggests that the orientation of this delicate, protruding structure mainly reflects the orientation of the humerus relative to geological pressures during diagenesis or folding. Therefore, the orientation of the crest is not a good indicator for taxonomy, phylogeny, or function. A unique feature only found in *Lufengosaurus* and PVL field number 6 is an inward kink in the course of the deltopectoral crest just proximal to its apex (fig. 7-5). A similarly shaped crest of the left humerus of *Plateosauravus* (SAM 3342) is probably deformed, since the crest of the right humerus of the same specimen is straight.

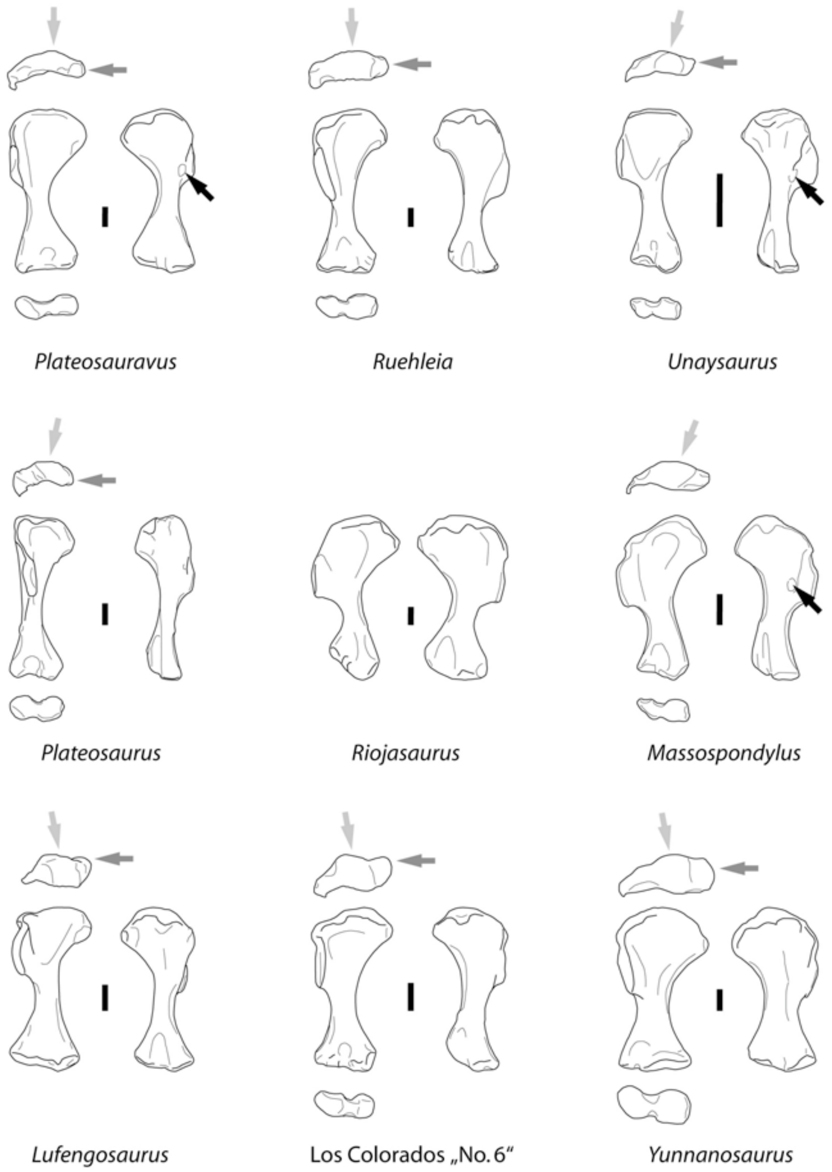

Figure 7-5. Comparison of the humeri of several ‘prosauropods’ in proximal (ventral down), ventral, distal (ventral up), and caudal views. Black arrows indicate the scar for the insertion of M. latissimus dorsi; medium grey arrows indicate the medial tuberosity; light grey arrows indicate the orientation of the humeral head. In *Lufengosaurus*, the distal end could not be observed because the specimen is mounted. For the same reason, both the proximal and distal ends of *Riojasaurus* cannot be shown adequately. Scaled to same humeral lengths; scale bar = 50 mm.

The distal ends of the humeri of most non-sauropod sauropodomorphs exhibit a prominent distocaudal facet that is significantly larger than in *Efraasia*; only in *Yunnanosaurus*, this facet is somewhat reduced. The grade of cranioventral torsion of the distal end relative to the main axis of the proximal end is around 45° in most ‘prosauropods’, but only about 30° in *Lufengosaurus*, PVL field number 6, and *Yunnanosaurus*. Differences are also found in the form and configuration of the ulnar and radial condyles. Both condyles are widely separated in *Plateosaura-*

vus, but they stand closer in other forms. Usually, the main axis of the radial condyle is angled ventrally relative to the main axis of the ulnar condyle, but this character is less clearly developed in *Plateosaurus* and PVL field number 6 (fig. 7-5). In most ‘prosauropods’, the radial condyle is somewhat smaller than the ulnar condyle, but the reverse is the case in *Lufengosaurus* and PVL field number 6. In *Plateosaurus*, both condyles are equally sized.

Antebrachium. In the antebrachium, interspecific variations are minor, and usually pertain to proportions (fig. 7-6). Radius and ulna of *Mussaurus* are especially elongate, slender bones (Bonaparte and Vince, 1979). In contrast to the basal-most sauropodomorphs (chapter 6), the cranial tubercle on the radius (‘biceps tubercle’) is more distally placed, at mid-length of the radial shaft. Moreover, its position has shifted laterally in *Plateosauravus*, *Anchisaurus*, and *Yunnanosaurus*. In *Massospondylus* and *Lufengosaurus*, the axis of the radial shaft is not perpendicular to the plane of the proximal articulation, but cranially angled. This character is pronounced in *Lufengosaurus* (fig. 7-6).

In lateral view, the caudal side of the shaft of the ulna is convexly curved in *Plateosauravus*, *Ruehleia*, and *Anchisaurus*, showing the plesiomorphic condition. The caudal side of the ulnar shaft is straight in *Unaysaurus* and *Riojasaurus*, but sigmoid in *Plateosaurus, Yunnanosaurus*, and *Massospondylus*, caused by a caudal deflection of the distal articular ends in these forms (fig. 7-6). Minor variations are also found in the form of the proximal end of the ulna, pertaining primarily to the size of the lateral process (which is much reduced in *Massospondylus*) and the length of the cranial process (which is elongate in *Yunnanosaurus*). The radioulnar articulation shows considerable differences: *Riojasaurus, Plateosaurus* and *Yunnanosaurus* have a tubercle on the craniomedial side of the distal ulna that articulates in a fossa caudolaterally on the distal radius, but the reverse is the case in *Unaysaurus*. *Plateosauravus*, *Massospondylus* and a number of other taxa exhibit a complex articulation with matching tubercles, ridges and fossae on both elements, while *Ruehleia* has no distinct radioulnar articulation at all. Moreover, the distal expansions of both radius and ulna are characterized by a complex arrangement of facets and tubercles immediately proximal to the rim of the articular cartilage. The presence of cartilage caps on the distal ends of the antebrachial bones is indicated by a roughened, pitted bone surface.

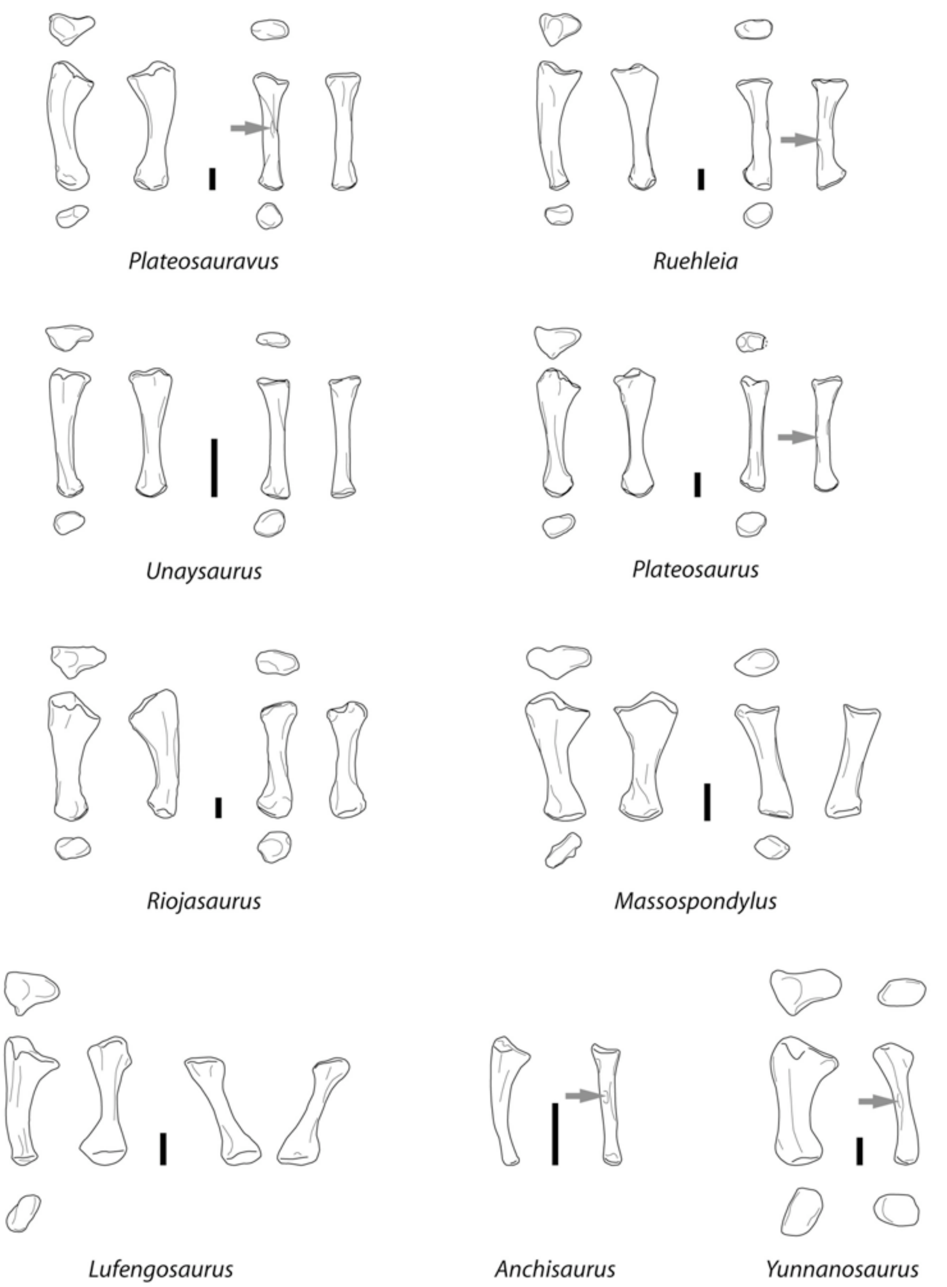

Figure 7-6. Comparison of the antebrachial elements of several ‘prosauropods’. For each taxon: left, ulna in proximal, lateral, distal, and medial views; right, radius in corresponding views. Proximal and distal views could not be fully observed in *Lufengosaurus* and *Anchisaurus*; in *Anchisaurus* and *Yunnanosaurus*, there was also no access to the medial sides of the bones. Grey arrows indicate the position of the cranial radial tubercle. Scaled to same ulnar lengths; scale bar = 50 mm.

The long axis of the distal end of the ulna of *Plateosaurus*, *Riojasaurus*, *Unaysaurus,* and *Massospondylus* is outwardly rotated, and forms an angle of about 30° with the long axis of the proximal cranial process. In *Ruehleia*, *Lufengosaurus*, and *Yunnanosaurus*, the long axis of the distal ulnar expansion is oriented almost perpendicular to that of the proximal cranial process. In *Plateosaurus* and *Coloradisaurus,* there is a conspicuous tubercle on the distal craniomedial edge of the radius. The distal articular surface of the radius has a suboval form with a pointed caudal corner in most 'prosauropods'. In *Riojasaurus* and *Coloradisaurus*, it has a pentagonal outline.

Manus. The record of 'prosauropod' hands (fig. 7-7) is not as complete as that of other forelimb elements. Complete hands are known from *Plateosaurus* (SMNS 13200, GPIT 1, and others), *Massospondylus* (BP/1/4998; BP/1/4934), *Lufengosaurus* (IVPP V15), *Anchisaurus* (YPM 1883), *Yunnanosaurus* (IVPP V20), and '*Plateosaurus* sp.' from Santa Cruz, Argentina (MLP 68-II-27-1; Casamiquela, 1977, 1980). Incomplete hands are preserved in '*Ammosaurus'* (UCMP 82961), *Ruehleia* (MB RvL 1), *Unaysaurus* (UFSM 11069), *Coloradisaurus* (PVL 3967), and *Mussaurus* (PVL 4210). Many of these specimens are still embedded in matrix, so that not all sides and articulations of the individual elements can be observed. In *Yunnanosaurus* and *Lufengosaurus*, the hands are mounted and partly covered with plaster.

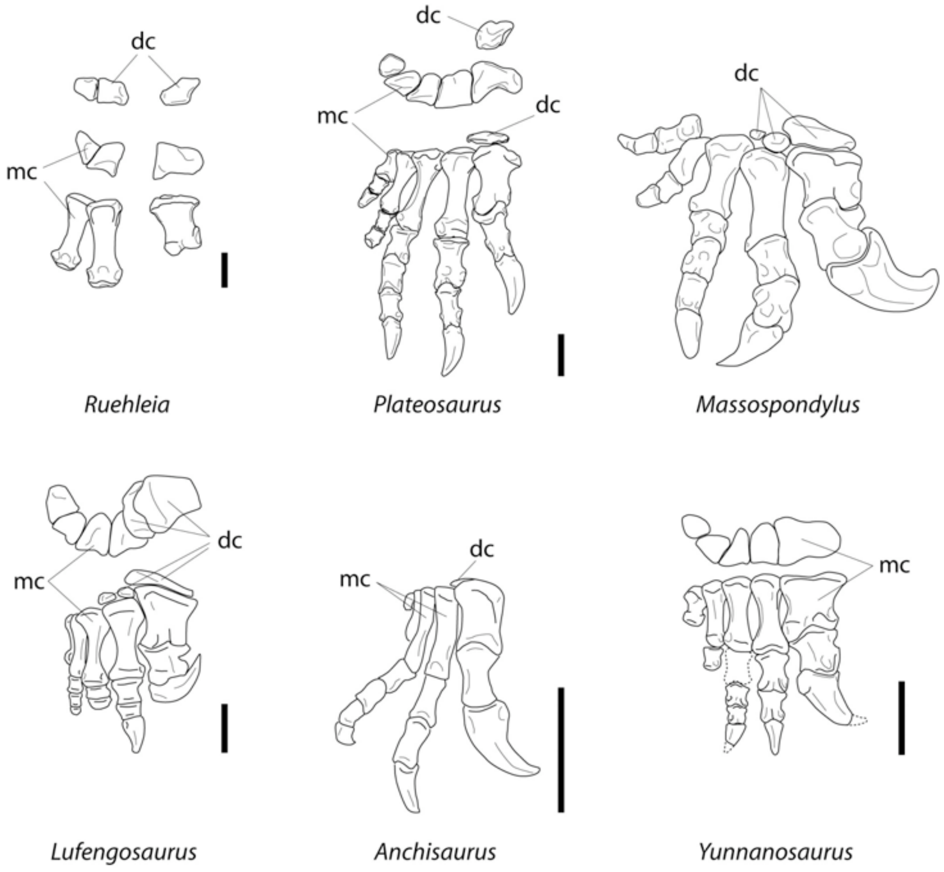

Figure 7-7. Comparison of 'prosauropod' hands in proximal views (above) and dorsal view (below). Scaled to the same length of metacarpal II for comparison of proportional differences; scale bar = 50 mm.

Like in *Thecodontosaurus*, no radiale and ulnare are known from more derived sauropodomorphs, even in fully articulated specimens. However, variable numbers of disc-like distal carpals have been found in *Ruehleia*, *Plateosaurus*, *Massospondylus*, *Lufengosaurus* and *Yunnanosaurus.* In *Ruehleia*, three elements cap metacarpals I–III, one for each metacarpal. These elements are convex proximally and concave distally, fitting on the proximal articular surface of the metacarpals. Distal carpal I is lozenge-shaped. In *Plateosaurus* (SMNS 13200) and *Anchisaurus* (YPM 1883), only distal carpal I is preserved, which is similar to the corresponding element of *Ruehleia*. However, distal carpals II to IV have been reported from a prosauropod hand assigned to *Plateosaurus* (Bonnan and Senter, 2007). In *Massospondylus,* distal carpal I is also similar to the same element of *Ruehleia*. Moreover, there is also a small, circular distal carpal II that is partially overlapped by distal carpal I, and a knob-like remnant of distal carpal III. Distal carpal II caps metacarpal II, while distal carpal III covers metacarpal III only partially (fig. 7-7). In '*Gryponyx africanus*' (SAM 3357-9, probably a junior synonym of *Massospondylus*; Galton and Cluver, 1976; Kitching and Raath, 1984), an even smaller, spherical element attaches proximolaterally to distal carpal III. In other specimens of *Massospondylus*, a similar element has been interpreted as an ossified intermedium (Cooper, 1981). Furthermore, fully articulated specimens of *Massospondylus* (including '*Gryponyx*') exhibit a wide gap between the antebrachial bones and the distal carpal row, implying the presence of cartilaginous proximal carpals in the living animal. In *Yunnanosaurus,* only distal carpal I is preserved; this element is rectangular and has a distolateral notch for reception of distal carpal II. The carpus of *Lufengosaurus,* which preserves distal carpals I and II, is similar.

In non-sauropod sauropodomorphs, two types of hands may be distinguished (fig. 7-7). The first type, which resembles *Thecodontosaurus* (chapter 6), is characterized by a metacarpal I that is significantly longer than wide, relatively slender metacarpals II and III, elongate phalanges, and the retention of four phalanges in digit III. This manual type is seen in *Anchisaurus*, *'Ammosaurus'*, *Plateosaurus, Mussaurus*, and MLP 68-II-27-1, and was present possibly also in *Ruehleia, Unaysaurus,* and *Efraasia*. The second type, which is seen in *Massospondylus*, *Lufengosaurus*, and *Yunnanosaurus*, is characterized by a metacarpal I that is as wide as long (or wider), robust metacarpals II and III, and phalanges that are only about as long as wide. In addition, *Lufengosaurus* and *Yunnanosaurus* retain only three phalanges in digit III. However, Young (1942) assumed that phalanx III.1 is missing in *Yunnanosaurus* (as shown in fig. 7-7). *Yunnanosaurus* (IVPP V20) is mounted with only an ungual on digit V, but given the size disparity between the articular surfaces of this element and metacarpal V, it is probable that there were two phalanges in this digit, like in all ‘prosauropods’ except *Thecodontosaurus* and probably *Anchisaurus*.

The individual metacarpals and phalanges vary in proportions, but are rather conservative in their characters. Metacarpal I is keyhole-shaped in proximal view and preserves asymmetric distal articular condyles. In *Massospondylus* and *Lufengosaurus*, metacarpal I is slightly inset into the carpus, being more proximally placed than the remaining metacarpals (fig. 7-7). Metacarpal I lacks extensor pits; on metacarpals II and III, these are only weakly developed (most distinct in *Ruehleia*). The distal ends of metacarpals II–IV have slightly dorsally rotated ligament pits, making these structures visible in dorsal view. Well-developed lateral flanges on the dorsoproximal corner of metacarpals I–IV slightly overlap the succeeding metacarpal dorsomedially. In articulation, the proximal ends of the metacarpals form a slight bow in *Plateosaurus, Yunnanosaurus*, and probably also in *Ruehleia*. In *Lufengosaurus*, the metacarpals are arranged in a semicircular structure (fig. 7-7); the available hands of *Massospondylus* are too compressed to assess the original curvature of the metacarpus.

The penultimate phalanges of ‘prosauropods’ exhibit proximally extending condyles on the dorsal side, indicating the ability to hyperextend the unguals. In *Massospondylus* and *Plateosaurus*, the distal condyles of phalanx I.1 have rotated ventrally in a way to keep the large ungual strongly flexed when the joint is in neutral position. In *Plateosaurus*, the distal condyles of all individual phalanges are asymmetrical build, with the lateral condylus extending further distally. A comparable asymmetry could not be observed in other ‘prosauropods’. The first ungual is always hypertrophied and strongly curved, but the unguals of digits II to V vary in relative width, length, and curvature. Moreover, the ungual of the first digit is characterized by an enormous flexor tubercle that makes up about one fourth of the dorsoventral height of this element.

Antetonitrus ingenipes and other stem-sauropods

Yates and Kitching (2003) shortly described the anatomy of *Antetonitrus*, but for a full understanding of the anatomical changes during the ‘prosauropod’-sauropod transition, a more detailed account on the forelimb morphology of this taxon is needed.

Scapula. Compared to other basal sauropodomorphs, the scapula of *Antetonitrus* is unusual (fig. 7-8). Like in *Yunnanosaurus*, the scapular blade is broadened relative to the scapular head. The blade is laterally flattened and rather short. The conspicuous distal expansion reaches a width of about 50% total scapula length. Moreover, the long axis of this expansion is not oriented perpendicularly to the long axis of the scapular blade like in other basal sauropodomorphs; instead, both axes form an angle of about 60°. Laterally, the blade bears an elongate facet on its proximal cranial border. A second, smaller facet is found distal to the former. Moreover, a distinct, 15 mm wide and 110 mm long flange protrudes from the proximal part of the caudal edge of the blade. A low swelling subdivides the lateral side of the distal expansion into a cranial and a caudal facet. The medial side of the distal half of the scapular blade is flattened and striated. Caudoproximally on the medial side, a wide, elongate depression extends medial to the caudal flange of the blade. The cranioproximal part of the medial blade is convex. Proximally, a triangular depression on the craniodorsal part of the scapular head extends somewhat onto the base of the blade (fig. 7-8).

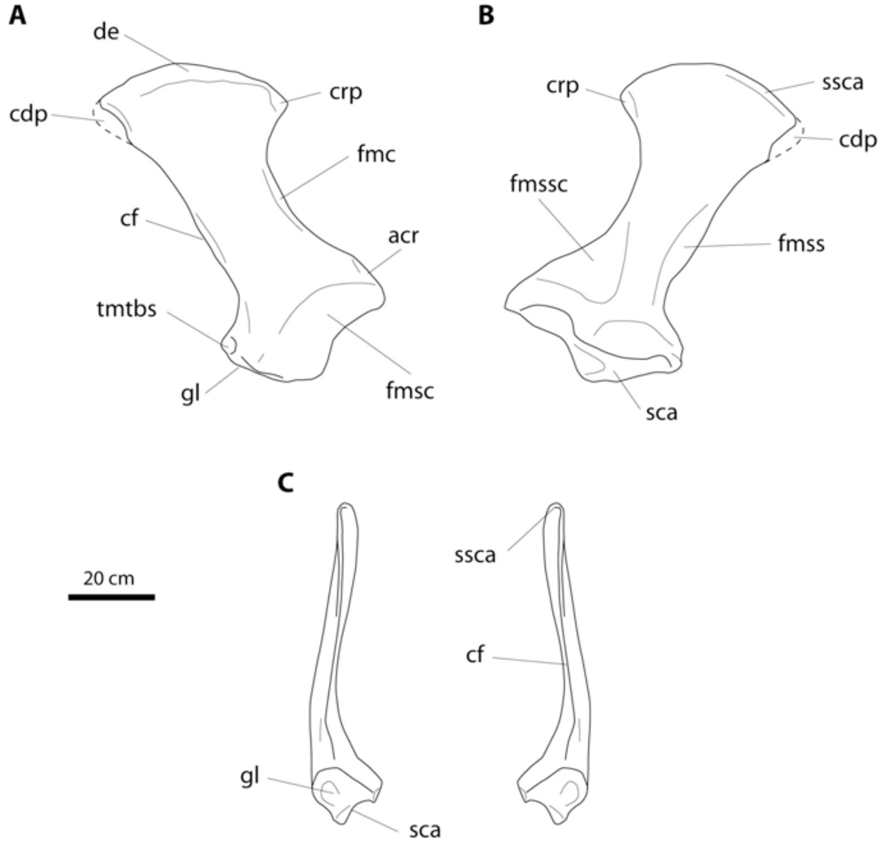

Figure 7-8. Osteological structures of the scapula of *Antetonitrus.* A, lateral view; B, medial view; C, reconstruction of the pectoral body profile in caudal view.

Caudolaterally on the scapular head, the oval scar dorsal to the glenoid (for attachment of M. triceps brachii caput scapulare) is caudally and slightly medially oriented. Cranial to the glenoid, the oval ventrolateral fossa is elongate and shows no differentiation into a caudal and a deeper cranial part. Craniodorsally on the scapular head, the acromial region is deep, but the clavicular articular facet is broken off. The angle between the acromion and the cranial edge of scapular blade is about 160°. The ventral edge of the scapular head (the suture with the coracoid) exhibits a distinct 'step'. The saddle-shaped scapulocoracoidal articular surface has a far ventrally extending lateral rim, but lacks tubercles or fossae.

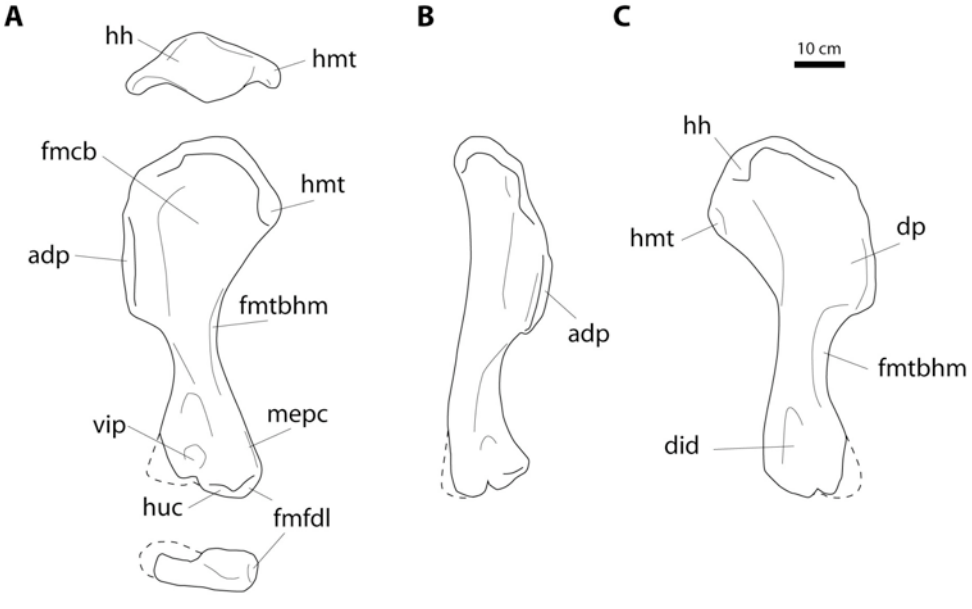

Figure 7-9. Osteological structures of the humerus of *Antetonitrus.* A, proximal (ventral side down), ventral, and distal (ventral side up) views. B, cranial view. C, dorsal view.

Humerus. The humerus of *Antetonitrus* is relatively elongate, compared to forms like *Massospondylus*, but retains many basal sauropodomorph features (fig. 7-9). The distal expansion is twisted about 30° cranially relative to the proximal end. Distally, the radial condyle is broken off. The humeral head is enlarged, almost hemispherical, and protrudes both above the (developmentally) dorsal and ventral sides of the shaft. In proximal view, the head has a subrectangular outline. In contrast to other 'prosauropods', the medial tuberosity is ventrally deflected, not dorsally as e.g. in *Lufengosaurus*. Cranially on the proximal end, the lateral tubercle is missing. The deltopectoral crest is large and extends for about 50% of the total length of the humerus. The crest is cranioventrally directed, but this might be caused partly by deformation. Both the proximal and distal bases of the crest gently curve towards the humeral head and distal shaft, respectively. The apex of the deltopectoral crest is elongate and protrudes cranially. On this side, the apex is dorsally bordered by a groove-like depression (the paramarginal groove). The apex is narrow in craniocaudal direction and tapers distally. A tubercle projects from its proximocaudal corner. The caudal side of the crest is concave. On the proximoventral part of the humerus caudal to the deltopectoral crest, there is a gentle, striated depression like in most archosaurs.

On the caudal side of the proximal humerus, a small tubercle protrudes immediately distal to the medial tuberosity. Distal to the level of the apex of the deltopectoral crest, the caudal side of the humeral shaft is flattened. In contrast to most ‘prosauropods’, there is no distinct ridge on the craniodorsal shaft dorsal to the deltopectoral crest. A narrow crest on the ventral side of the shaft runs obliquely from the distal base of the deltopectoral crest towards the cranial corner of the ulnar condyle. Craniodistally to this crest, a triangular depression extends distally. The deep ventral intercondylar pit is situated in the distal part of this depression. The entepicondyle is caudodorsally placed and reduced to a low, elongate elevation. An ectepicondyle cannot be delimited. In distal view, the ulnar condyle is suboval with straight dorsal and ventral edges. The large, concave distocaudal facet forms an angle of about 45° to the plane of the distal condyles. Since the radial condyle is broken off, there is no clue if its long axis formed an angle to the long axis of the ulnar condyle like in most basal sauropodomorphs. The dorsal side of the distal expansion exhibits a weakly developed intercondylar depression.

Antebrachium. The ulna of *Antetonitrus* resembles that of other basal sauropodomorphs (fig. 7-10). The lateral process is robust and the cranial process short and narrow, but not significantly more so than e.g. in *Plateosauravus*. Caudally on the proximal end, there is a domed, rugose area like in other ‘prosauropods’. The caudal side of the shaft is only slightly curved. On the cranial edge of the distal end, a large tubercle for articulation with the radius protrudes craniomedially, accompanied by a cranially adjacent furrow. The distal end is twisted about 10° cranially relative to the long axis of the proximal cranial process. On the medial side of the proximal end, a wide depression extends distally. The radial fossa cranial to the lateral process has a triangular shape. In cranial view, a small tubercle (probably for the insertion of M. biceps brachii) protrudes about 50 mm distomedially to the cranial process. Caudal to the lateral process, a wide fossa extends distally along the ulnar shaft. The caudal side of the distal expansion is characterized by a large, pitted tubercle that merges with the proximally extending distal articular surface.

The shaft of the radius is transversely flattened. The distal end of the radius is oriented almost in parallel to the long axis of the proximal end. The medial side of the shaft is smooth and flattened. A low, pitted tubercle projects from the caudolateral side of the proximal end. The cranial and caudal edges of the shaft are rounded and lack distinct intermuscular ridges. A large, rugose ‘biceps tubercle' is situated on the cranial edge of the shaft, right distal to the proximal third of the radius. Distal to this tubercle, the lateral shaft exhibits two facets. The distocranial facet is narrow and craniolaterally oriented, while the distocaudal facet is wider and laterally directed. The caudal side of the distal end of the radius bears a huge tubercle that tapers proximally. Both laterally and medially, this tubercle is bordered by grooves.

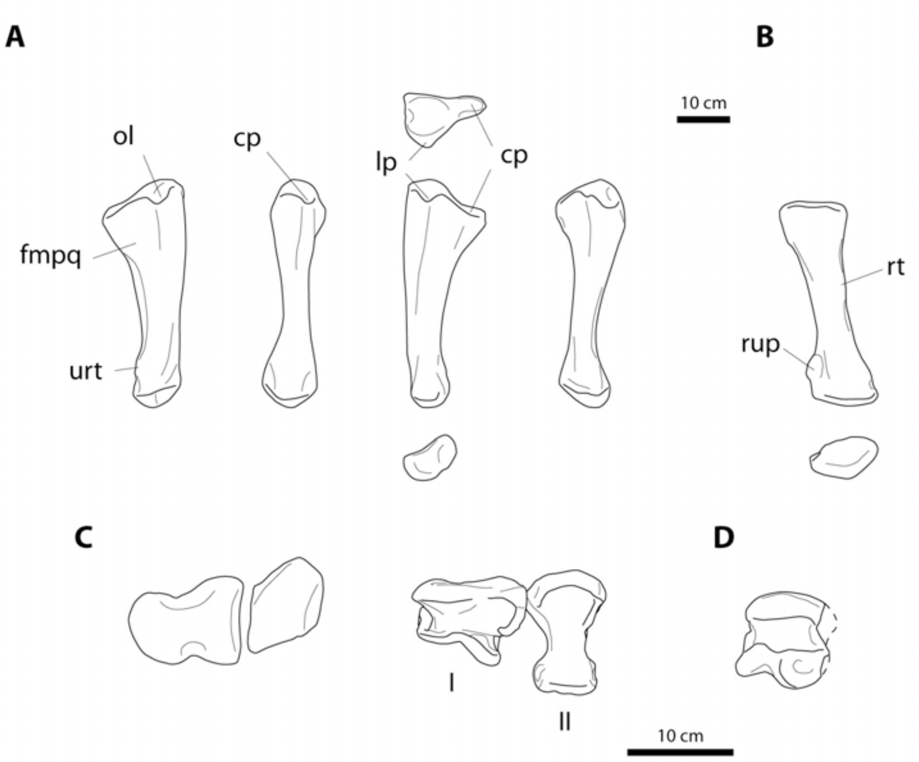

Figure 7-10. Osteological structures of the antebrachium and metacarpus of *Antetonitrus*. A, ulna in medial, cranial, proximal, lateral, distal, and caudal views. B, radius in lateral and distal views. C, metacarpals I and II in proximal (left) and dorsal (right) views. D, phalanx I.1 in dorsal view.

Metacarpus. The holotype of *Antetonitrus* preserves only metacarpals I and II. Metacarpal I is proximodistally compressed and wide relative to its length; metacarpal II is robustly build (fig. 7-10). Therefore, the hand of *Antetonitrus* resembles manual type 2 of other ‘prosauropods’ (see above). Both metacarpals exhibit the same characters as those of other basal sauropodomorphs; the closest resemblance is with *Yunnanosaurus*. Metacarpal I retains strongly asymmetric distal articular condyles that lead to a medial deflection of the proximal phalanx during extension, and a lateral deflection during flexion. Both medially and laterally, the condyles bear deep ligament grooves. Metacarpal II is specialized in showing no clear differentiation of the distal end into two separate condyles; instead, the articular surface for the proximal phalanx resembles a simple reel. Ligament grooves are present on both sides, but are weakly developed. There is no trace of an extensor pit on the dorsal side of the distal shaft.

The second basal sauropodomorph taxon regarded as closely related to the earliest sauropods is *Melanorosaurus*. After a confused taxonomic history, Galton et al. (2005) proposed a neotype for this genus, NM QR3314. The forelimb anatomy of this specimen was recently described and discussed in detail by Bonnan and Yates (2007). For a detailed description, the reader is therefore referred to that work. NM QR3314 is the only *Melanorosaurus* specimen that preserves a complete, articulated forelimb; other referred specimens are incomplete or of doubtful taxonomic assigment (van Heerden and Galton, 1997; Galton et al., 2005). However, in NM QR3314 the bone surfaces are heavily damaged, and provide not much information on muscle attachment sites.

Like in *Yunnanosaurus* and *Antetonitrus*, the scapular blade is broad relative to the craniocaudal length of the scapular head. The left ulna, one of the best-preserved forelimb elements of this specimen, is not markedly different from the corresponding element of other prosauropods (fig. 7-11A). Most significant in NM QR3314 is the virtually complete preservation of the right manus (fig. 7-11B). The preserved phalangeal formula is 2-3-4-1-1; however, another unidentified bone distal to phalanx V.1 possibly represents a reduced phalanx IV.2 or V.2 (not mentioned by Bonnan and Yates [2007]). Metacarpal I is wide and short, metacarpals II–IV are robust, and the phalanges are blocky. Moreover, the phalanges between the proximal phalanx and the ungual are considerably reduced in size. The manus resembles that of *Yunnanosaurus* most closely, but metacarpals IV–V and the distal phalanges are more reduced. No carpal element could be identified. Overall, the hand of *Melanorosaurus* belongs to 'prosauropod' manual type 2 (see above).

Other basal sauropodomorphs that stand close to the origin of sauropods and preserve forelimb elements include *Jingshanosaurus* (fig. 7-11C), *Chinshakiangosaurus*, and *Gongxianosaurus* (fig. 7-11D). The latter form is currently regarded as most significant for the 'prosauropod'-sauropod transition (Upchurch et al., 2004), and will be addressed in more detail in chapter 8. Unfortunately, none of these taxa could be included in the present study; hence, only a brief summary of their anatomy is presented here, based on published descriptions (Zhang and Yang, 1995; He et al., 1998; the forelimb elements of *Chinshakiangosaurus* have not been described or figured yet). Shared characters of *Jingshanosaurus* and *Gongxianosaurus* include a strongly curved cranial edge of the scapula; a prominent distal expansion of the scapula, with a pronounced caudodistal corner; and an enlarged coracoid that almost doubles the size of the scapular head. The humerus of *Jingshanosaurus* is markedly robust. It bears a strong deltopectoral crest that extends for more than 50% of the length of the humerus, closely resembling *Yunnanosaurus* in this respect. Moreover, it has a triangular ventral intercondylar depression, and a large distocaudal facet (possibly for the origin of M. flexor digitorum longus).

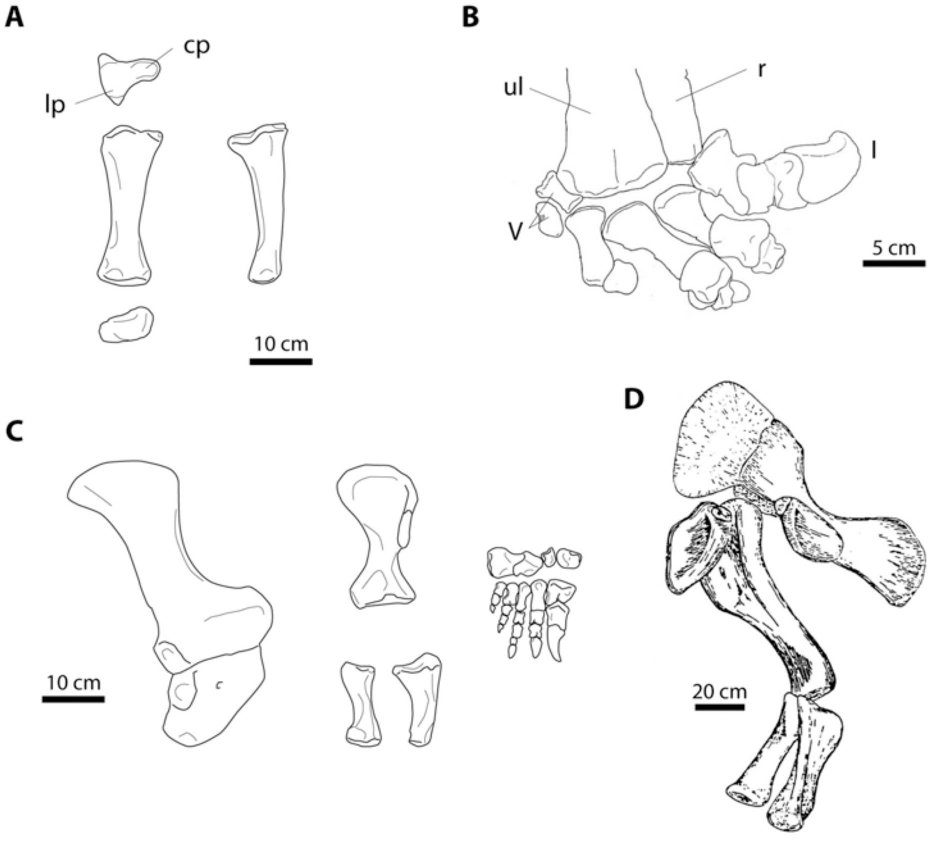

Figure 7-11. Comparison of forelimb material of several ‘prosauropods’ that are regarded as closely related to Sauropoda. A, ulna of *Melanorosaurus* (NM QR3314) in proximal, medial, distal, and lateral views. B, manus of NM QR3314, *in situ* preservation; modified from Bonnan and Yates (2007). C, interpretative sketches of the forelimb elements of *Jingshanosaurus*, based on photographs in Zhang and Yang (1995). D, forelimb of *Gongxianosaurus* as found *in situ*; modified from He et al. (1998).

Based on the drawings of He et al. (1998), the distal end of the elongate humerus of *Gongxianosaurus* is not as expanded as in ‘prosauropods’, but resembles the sauropod condition (see chapter 8). However, *Gongxianosaurus* preserves a well-developed deltopectoral crest on the humerus. The type material of *Gongxianosaurus* also contains a pair of sternal plates that exhibit a straight medial margin and a thickened cranial process.

In *Jingshanosaurus*, the antebrachial elements are rather short and stout, like in *Yunnanosaurus*. *Jingshanosaurus* is unique in comprising three carpal elements that have been identified as intermedium, distal carpal I, and fused distal carpals II–V (Zhang and Yang, 1995). The complex, irregularly shaped block of distal carpals II–V is probably not pathologic, since both the left and the right manus show this feature. The hand can be assigned to manual type 2. However, metacarpals II and III are reduced in length, and measure only slightly more than metacarpal I. The manual phalangeal formula of *Jingshanosaurus* is 2-3-4-3-2.

Muscle reconstructions

Based on the results of the previous chapters, the shoulder girdle musculature is reconstructed here for *Unaysaurus, Lufengosaurus*, and *Antetonitrus*. Moreover, parts of the antebrachial musculature of *Plateosaurus* are inferred. The reconstruction of the myology of *Antetonitrus* will be discussed in detail in the following paragraphs. The remaining reconstructions are based on the same principles, because not many differences in the topology of muscle attachments can be recognized in basal sauropodomorphs.

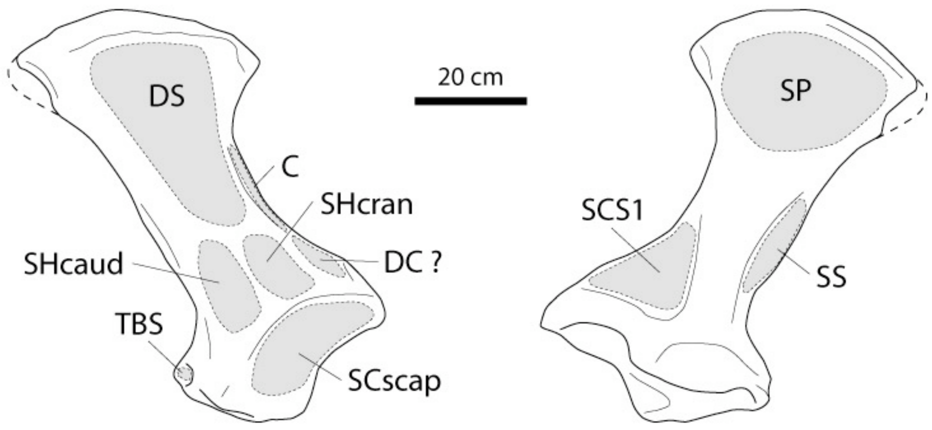

Figure 7-12. Reconstructions of the muscular attachments on the scapula of *Antetonitrus*. Left, lateral view; right, medial view. For explanations see text.

Scapulocoracoid. In *Antetonitrus*, the configuration of the scapular muscles closely resembles *Saturnalia* and *Efraasia* (fig. 7-12). Differences are primarily due to the deviant proportions of the scapular blade. The shortening of the blade led to a comparatively smaller area of origin of M. deltoideus scapularis. The partitioning of the lateral side of the distal expansion into two facets possibly indicates the presence of a M. teres major. However, since the plesiomorphic osteological correlate of this muscle could not be identified on the humerus, its course is not reconstructed here. In *Massospondylus*, a large scar on the dorsal side of the humerus indicates the insertion of M. latissimus dorsi and M. teres major, like in all archosaurs plesiomorphically (chapter 3). Possibly, the caudodistal process of the scapular blade correlates to the origin of this muscle (fig. 7-15; see chapter 6).

The considerable shortening of the cranial edge of the scapular blade reduces the area for the insertion of M. cucullaris and M. levator scapulae. The elongate facet on the proximocranial edge of the blade probably served for the insertion of M. cucullaris, as inferred for *Euparkeria* and basal dinosaurs (chapters 4–6). As a consequence, the area of insertion of M. levator scapulae appears to be significantly reduced. Moreover, the strong curvature of the distocranial edge of the scapular blade would have led to an inefficient angle of insertion of M. levator scapulae, unless the neck was held level with or below the distal expansion of the scapula.

The relatively broad base of the scapular blade provides much room for the origins of Mm. scapulohumerales, but like in all basal archosaurs, there are no osteological correlates that would allow for a delimitation of their attachment sites (chapters 4–6). The dorsoventrally deep acromial region between the ventral fossa and the dorsal border of the scapular head possibly served as a secondary origin of M. deltoideus clavicularis. If the clavicles were reduced in *Antetonitrus*, the muscle might also have had its origin solely from this area. The position and relative size of the ventrolateral fossa on the scapular head is plesiomorphic. Like in all archosaurs (chapter 3), the origin of M. triceps brachii caput scapulare is indicated by a circular scar dorsal to the glenoid, and exhibits no significant modifications.

On the medial side of the scapular blade, the area for the insertion of M. serratus profundus is somewhat reduced. Paralleling the reduction of the area of origin of M. deltoideus scapularis, this is a consequence of the shortening of the scapular blade. Like in other basal dinosaurs, the elongate facet medial to the caudal flange of the scapular blade probably served for the attachment of M. serratus superficialis (chapters 4–6). The considerable elongation of the caudal flange may correlate to a stronger Ligamentum sternoscapulare internum (which in turn may be related to a more powerful M. triceps brachii caput coracoscapulare), but this inference is rather speculative. Cranially on the medial side of the scapula, the triangular facet that indicates the origin of M. subscapularis is slightly enlarged relative to the size of the scapular head. Like in *Saturnalia* and *Efraasia,* it is situated far ventrally, and does not extend much onto the scapular blade.

The coracoid musculature of basal sauropodomorphs remained largely plesiomorphic, as far as can be inferred (see fig. 7-14). The most significant difference is the enlargement of the biceps tubercle, probably correlating to an exceptionally powerful M. biceps brachii. The sites of attachment of the remaining muscles show no obvious modifications. The significance of the varying form of the subglenoid fossa (the attachment of M. costocoracoideus) cannot be explained, since the origin of this muscle on the sternal ribs and cartilaginous sternum is not preserved in any basal sauropodomorph.

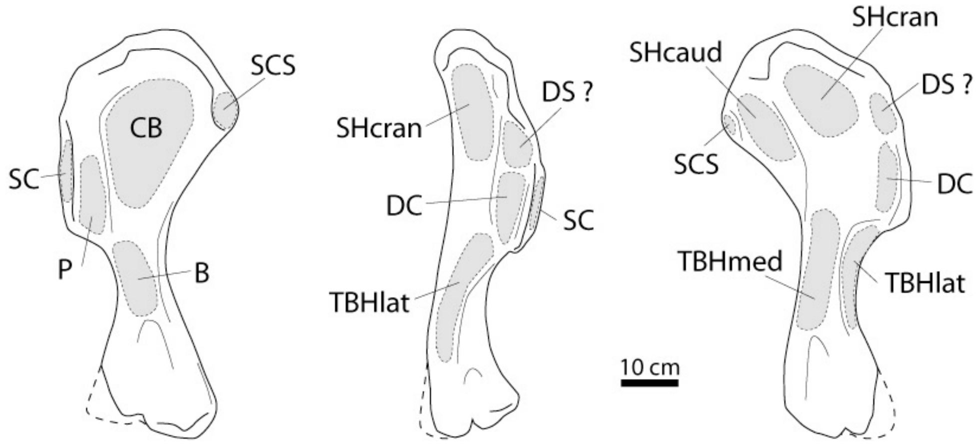

Figure 7-13. Reconstructions of muscle attachment sites on the humerus of *Antetonitrus*. From left to right, ventral, cranial, and dorsal views. For explanations see text.

Humerus. Although different in shape from the humeri of basal-most sauropodomorphs, the humerus of *Antetonitrus* lacks traces of major modifications of the musculature (fig. 7-13). Nevertheless, there are two main differences. First, the loss of the lateral tubercle, accompanied by the reduction of the wide depression between this tubercle and the apex of the deltopectoral crest, led to a considerably smaller attachment site for M. deltoideus scapularis. This might be correlated to the reduction of the origin of this muscle on the scapula (see above), but such a causal connection is speculative. Second, in *Antetonitrus* and many other basal sauropodomorphs, there is no trace of the oval scar that indicates the insertion of

M. latissimus dorsi and M. teres major. This may be explained with a reduction, or these muscles evolved a fleshy instead of a tendinous insertion (see Discussion below). Regarding the remaining muscles, the expanded proximal part of the humerus provided much room for the insertion of the Mm. scapulohumerales. The shortening and constriction of the humeral shaft led to a reduction of the probable areas of orgin of Mm. triceps brachii capiti humerales and M. brachialis. However, the ventral border of the origin of M. brachialis is probably indicated by the narrow crest dorsolaterally to the ventral intercondylar depression. The muscle attachment sites on the medial tuberosity and deltopectoral crest show the plesiomorphic configuration (see chapter 6). Similar conditions are also found in other 'prosauropods' (fig. 7-15). The epicondylar muscles lack osteological correlates that can be identified unequivocally, a problem already addressed in the previous chapter.

The musculature of the antebrachium, as inferred from osteology, shows no significant modifications relative to the basal-most sauropodomorphs (chapter 6; figs. 7-14, 7-16). One exception is the cranial tubercle of the radius ('biceps tubercle'), which possibly indicates the insertion of M. brachialis (chapter 5). The significance of the modifications of this structure is discussed in the following section.

Discussion

Osteology and *bauplan*

Scapulocoracoid. Phylogenetic bracketing (with *Euparkeria*, *Massospondylus*, and extant Theropoda as outgroup taxa) as well as the basic similarity of the scapulocoracoidea implicate that the *bauplan* of the pectoral girdle observable in *Massospondylus* (fig. 7-2) probably also applies to all other taxa treated so far (chapters 4–6). An alternative configuration with more widely spaced, laterally oriented coracoids may be conceivable if the clavicles were completely lost. However, facets for clavicular articulation are retained on the acromion of most basal dinosaurs and sauropodomorphs. This indicates that clavicles were originally present at least in an unossified state, but are just rarely preserved in the fossil record (see von Huene, 1926; Cooper, 1981; Galton, 1990; Padian, 1997b; Galton and Upchurch, 2004; Yates and Vasconcelos, 2005; compare also Bryant and Russell, 1993). Moreover, even in archosaurs with reduced clavicles (i.e., crocodilians), the coracoids still articulate close to the midline. Instead of broadening the episternal process, crocodilians evolved elongate coracoids to obtain a derived, transversely wide body profile. A similar phenomenon can be observed in birds, where the extremely elongate coracoids are still almost in contact medially on the cranial rim of the sternum (e.g., Bellairs and Jenkin, 1960; Baumel and Witmer, 1993). Possibly, this constraint of mid-line placement of the ventromedial edge of the coracoid constitutes a hint towards ontogenetic principles that apply to all archosaurs.

As noted above, the ventral orientation of the coracoid leads to a caudolateral, not strictly caudal orientation of the coracoidal part of the glenoid. Therefore, the pectoral girdle is able to receive horizontally directed forces, while the scapular portion of the glenoid primarily buffers vertically directed forces. The strong buttress on the medial side of the scapular head in most ‘prosauropods’ demonstrates the ability of the pectoral girdle to resist compression, which would be exerted on the girdle when the limb transfers ground reaction forces during locomotion or standing. However, it is to note that such a buttress is also present in obligate bipedal forms (e.g., *Dilophosaurus*, see chapter 5); therefore, it indicates only a constructional property, not the preferred locomotory behavior of basal sauropodomorphs.

The proof that the coracoids almost contacted each other in midline implies that the main part of the sternum and the sternal plates were positioned caudally to these elements, not medially. In this position, the sternum would articulate with the caudomedial corners of the coracoids. In fossil specimens, a thick, rugose rim is usually present in this region of the coracoid (von Huene, 1926; Galton, 1990; Galton and Upchurch, 2004). Moreover, in all extant tetrapods, the main axis of the sternum is oriented in parallel to the vertebral column. It is assumed here (and taken into account for the reconstructions) that sauropodomophs also possessed a spine-parallel orientation of the sternum. In *Plateosaurus,* sternal ribs articulated primarily with dorsal ribs 3 to 5, as indicated by the thickened, rugose distal ends of these dorsal ribs (von Huene, 1926). Although the shapes of the sternal ribs (and in most cases even of the dorsal ribs) are unknown in basal sauropodomorphs, there are no hints towards specializations where dorsal ribs are known, supporting a plesiomorphic position and orientation of the sternum in these forms. Considering the form of the coracoid and the angle between scapular blade and head, the cranial part of the ventral shoulder girdle curves dorsally away from the plane of the sternum in all known sauropodomorphs that are more derived than *Saturnalia*. This effect is the first step towards the transformations seen in sauropods (chapter 8), and will be discussed in length under the topic ‘scapulocoracoid orientation’ in chapter 9.

The varying position of the caudal flange of the scapular blade is hard to explain. A more distal position may be related to a more caudal course of the Ligamentum sternoscapulare internum relative to the glenoid joint, which in turn may alter the origin of M. triceps brachii caput coracoscapulare. However, this assumption is hard to test, and the significance of such a modification is unknown. Therefore, the position and size of the caudal flange may be important for taxonomic and phylogenetic analyses, but its function remains a mystery. The same applies to the variations in the form of the distal edge of the scapular blade.

The enormous size of the biceps tubercle on the coracoid indicates the necessity of a stable bony anchor for the fibres of this muscle (see Wolff, 1892; Hoyte, 1966; Frost, 1990), which apparently exerted strong tensional forces on its attachment. A hypertrophied forearm flexor would not have been necessary for quadrupedal locomotion, even in a sprawling posture, since flexion occurs primarily during the protraction phase of a gait (Hildebrand and Goslow, 2001; Liem et al., 2001), when the limb is in the air. In the support phase, when work against gravity has to be done, flexion would actually be counterproductive. In ‘prosauropods’, the obviously strongly developed M. biceps brachii served therefore for powerful flexion of the forearm in bipedal stance, e.g. for manipulating tree branches during feeding, a behavior suggested previously by several authors (Galton, 1990; van Heerden, 1997; Upchurch, 1997a; Galton and Upchurch, 2004).

Humerus. The doming of the humeral head seen in many basal sauropodomorphs, including *Antetonitrus*, may relate to a greater maneuverability of the humerus. Taxa that lack a significant doming of the head (like *Unaysaurus* and *Plateosaurus*) seem to be considerably restricted in moving the humerus in the glenoid joint (Bonnan and Senter, 2007). However, the range of motion of the humerus depends on many factors, including the form of the glenoid, the shape of the unpreserved cartilage caps of both humerus and glenoid, the configuration of the ligaments and articular capsule that surround the joint, and the course of the musculature acting on the humerus (see Haines, 1939b, 1952).

The conspicuous rotation of the medial tuberosity observed in *Lufengosaurus* and PVL field number 6 places the point of attachment of M. subcoracoscapularis somewhat dorsal to the pivot of the humerus, while in other ‘prosauropods’, the insertion is more or less in line with the long axis of the proximal expansion of the humerus. This specialization parallels a development seen in theropods (chapter 5) and probably indicates a more parasagittal orientation of the humerus, with a craniomedially directed deltopectoral crest. The unusual form of the proximal base of the crest, as well as the lateral shift of the caudal (developmentally dorsal) part of the humeral head in *Lufengosaurus* might also correlate to this reorientation. However, the coracoidal portion of the glenoid remains large and partly laterally oriented. Therefore, it may be concluded that *Lufengosaurus* was able to abduct the humerus significantly from the parasagittal plane (fig. 7-14), rendering the optimization of parasagittal retraction an additional ability that does not necessarily exclude body support in semi-erect stance. The issue of humerus posture is strongly connected with the problem of manus pronation in 'prosauropods', which will be discussed below.

Interestingly, the proximal end of the humerus of *Antetonitrus* lacks a modification comparable to that seen in *Lufengosaurus*. Instead, it preserves the plesiomorphic, ventrally open bow that is also found in *Saturnalia* and *Plateosauravus*. On the other hand, the domed humeral head that extends on the developmentally ventral side of the shaft might correlate to a greater maneuverability, and possibly also allowed for a vertical orientation of the humerus. However, this depends strongly on the form and orientation of the coracoid and its glenoid portion, which are not preserved in *Antetonitrus*.

On the developmentally dorsal side of the humerus, the loss of the scar for insertion of the tendon of M. latissimus dorsi and M. teres major is puzzling. The distribution of such a scar in 'prosauropods' appears to be random; for example, it is present in *Plateosauravus* and *Unaysaurus*, but misses in the probably closely related and well-preserved *Ruehleia*, which nevertheless has a very similar shape of the humerus. The most plausible explanation is that the M. latissimus dorsi / M. teres major system developed a fleshy type of insertion in many basal sauropodomorphs, including *Antetonitrus*. Since these mucles are important abductors of the humerus and antagonists of M. coracobrachialis, a complete loss is unlikely. A fleshy insertion of M. latissimus dorsi / M. teres major would have been a novelty that is unknown in most extant non-avian diapsids (chapter 3), and probably indicates an altered function of these muscles. However, the type of insertion provides no clues regarding mechanical advantages, if the physiological properties of the inserting muscles are unknown (An et al., 1984; Gans, 1988). Therefore, this evolutionary novelty cannot be connected to adaptations for grasping or locomotion, and remains unexplained.

The modifications of the distal end of the humerus resembles the development seen in theropods in two respects (see also chapter 5): first, the enlargement of the distocaudal facet between ulnar condyle and entepicondylus, which possibly correlates to the origin of M. flexor digitorum longus; second, the outward twist of the distal expansion. Like in theropods, the enlargement of the origin of M. flexor digitorum longus possibly indicates that this muscle was powerful, and might be correlated to improved grasping adaptations in the hand. The presence of huge flexor tubercles on the unguals (especially in digit I) supports this explanation. The outward (= developmentally cranial) rotation of the distal expansion inflicts a permanent supination of the hand if the antebrachium is in neutral position. Paralleling theropods, this may also be interpreted as an adaptation for effective grasping (von Huene, 1926; Galton, 1971b; Raath, 1977; Carpenter, 2002; Senter and Robins, 2005; Senter, 2006, 2007; Bonnan and Senter, 2007; chapter 5). However, since the grade of humeral torsion varies among basal sauropodomorphs, the ability to supinate the hand appears to have been differently developed. Large forms, like *Lufengosaurus* and *Antetonitrus*, exhibit a less pronounced twist; hence, manus pronation during quadrupedal locomotion was facilitated (see below).

The different shapes of the distal articular ends of basal sauropodomorph humeri also relate to this issue. Radius and ulna usually do not fully articulate proximally in extant quadrupedal diapsids; instead, the configuration of the distal condyles of the humerus gives a better idea of the natural articulation of these bones than the form of the radial fossa on the proximal ulna (Haines, 1946; Landsmeer, 1983, 1984; *contra* Bonnan and Yates, 2007). In basal forms like *Plateosauravus,* the widely spaced ulnar and radial condyles, and the caudal deflection of the radial condyle relative to the axis of the ulnar condyle enabled the radius to rotate somewhat around the ulna. Therefore, these animals were able to pronate the hand to a certain degree. In *Plateosaurus,* the closely adjacent, equally sized condyles probably lessened this ability significantly (see von Huene, 1926; Bonnan and Senter, 2007).

Antebrachium. Different capabilities to pronate the manus are also reflected in the shape of the radius. In *Lufengosaurus* and *Antetonitrus,* the acute angle between the proximal cotyle and the axis of the shaft places the distal end of the radius cranially and slightly medially to the distal end of the ulna (fig. 7-14), which is facilitated by the plesiomorphic form and orientation of the radial condyle (see above). *Massospondylus* exhibits comparable adaptations, albeit weakly developed. The meaning of these observation for the evolution of locomotion in basal sauropodomorphs will be discussed in length in chapter 9.

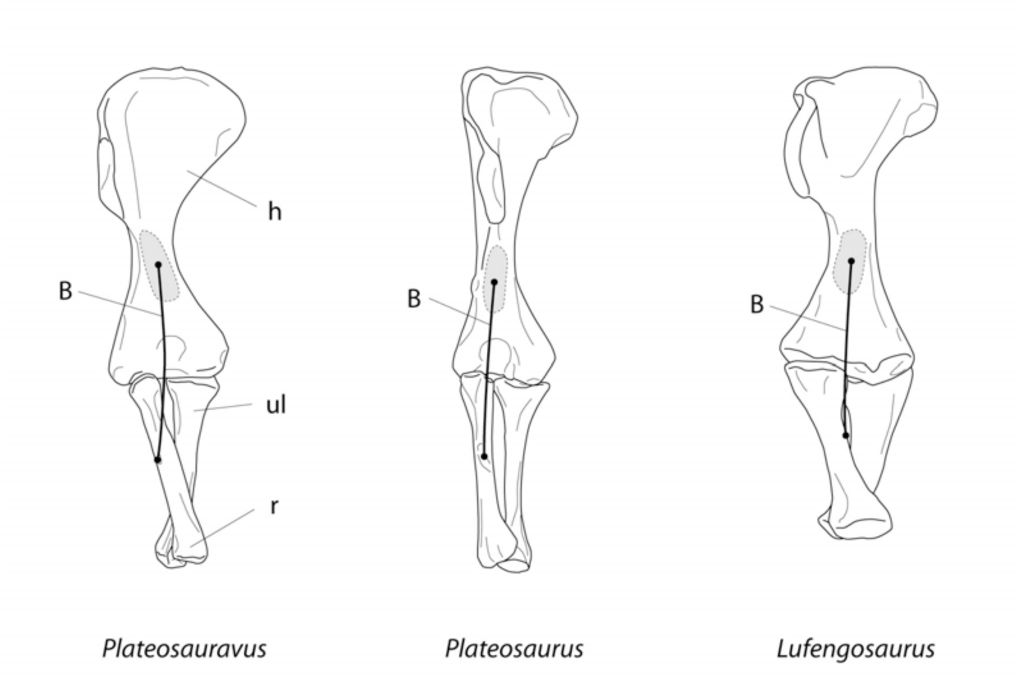

Figure 7-14. Different adaptations to partially pronate the hand in the basal sauropodomorphs *Plateosauravus* and *Lufengosaurus*, compared to *Plateosaurus*. Not to scale. For explanations see text.

The lateral shift of the cranial radial tubercle in *Plateosauravus*, *Anchisaurus*, and *Yunnanosaurus* probably represents a different solution for the problem of manus pronation. The difficulties of a proper reconstruction of the musculature that inserted on this tubercle have already been discussed in chapter 5. If the hypothesis were correct that the tubercle served primarily for attachment of M. brachialis, a lateral shift of this insertion would rotate the radius around its long axis when this muscle contracts, placing its distal end craniomedially to the ulna (fig. 7-14). In forms like *Plateosaurus* that have a plesiomorphic form of the radius and a narrow elbow joint, such a rotation is severly hampered (Bonnan and Senter, 2007). Nevertheless, both pronation systems do not permit a directly cranial orientation of the dorsal side of the manus when the humerus is held vertically. Instead, the inner digits would have touched the ground only if the humerus was held in a semi-erect posture, and even then the main axis of the hand would have been craniolaterally, not strictly cranially directed. The ichnotaxon *Navahopus* (Baird, 1980), which was attributed to *Anchisaurus*, supports this reconstruction by exhibiting manual prints with a craniolateral orientation of digit III and a gauge that is significantly wider than that of the pedal prints, despite the narrowness of the pectoral girdle. Moreover, in *Antetonitrus* a semi-erect pose of the humerus during support is indicated by the retention of a ventral intercondylar cavity, which probably served for storing synovial fluid during compression of the elbow joint (see chapter 6; *contra* Bonnan and Yates, 2007, who assumed this cavity ['cuboid fossa'] in *Melanorosaurus* to have received the radius during strong flexion of the forearm).

Manus. Distally in the antebrachium, the complex form of the radioulnar articulation probably enabled sliding articulation and simultaneously stabilized the wrist, if the hand was used as a grasping tool and therefore had to be supinated and pronated against the resistance of the manipulated matter (e.g., branches). In sauropodomorphs, this was especially important since radiale and ulnare do not ossify, but the significance of this latter adaptation is unclear. The structure of 'prosauropod' hands, like the rest of the forelimb, exhibits clear adaptations to grasping, an issue already examined by a various authors (von Huene, 1905, 1926; Lull, 1953; Charig, 1965; Galton, 1984b, 1990; Upchurch, 1997; Galton and Upchurch, 2004). However, forms with adaptations for manus pronation in the antebrachium usually exhibit the modified manual type 2, with a wide metacarpal I, robust metacarpals II–IV, and block-like phalanges. These include *Lufengosaurus, Yunnanosaurus, Antetonitrus*, and also *Massospondylus*. *Anchisaurus* combines a plesiomorphic hand structure with a laterally displaced radial tubercle, and is therefore an exception from this pattern. Nevertheless, the modifications seen in Massospondylinae and more derived sauropodomorphs are clearly advantageous if the hand is used for locomotion, but not for grasping. This latter assessment is corroborated by the discovery of obligate quadrupedal hatchlings of *Massospondylus* (Reisz et al., 2005).

Myology

With these interpretations of the osteological modifications in mind, reconstructions of parts of the skeletomuscular system of the forelimbs of *Unaysaurus*, *Lufengosaurus* (fig. 7-15), *Plateosaurus* (fig. 7-17), and *Antetonitrus* (fig. 7-16) will be discussed in the following.

Since the attachment sites for the cingulo-axial muscles show no significant modifications, it is assumed here that in all basal sauropodomorphs these muscles had a configuration similar to that reconstructed for *Saturnalia* (see fig. 6-12). One possible exception is the M. cucullaris / M. levator scapulae system in *Antetonitrus*: The facet that probably indicates the insertion of one or both of these muscles is more cranially than dorsocranially oriented, and a caudoventral course of these muscles would be hampered by the protruding distocranial corner of the scapular blade. Therefore, it is possible that the modification of the shape of the scapular blade seen in *Antetonitrus* and more derived sauropodomorphs like *Gongxianosaurus* (and to a lesser extent also in *Jingshanosaurus*) is related to a modified, more horizontal neck posture. However, the neck of *Antetonitrus* is largely unknown, and basal eusauropods like *Patagosaurus* lack this modification of the scapular blade (see chapters 8 and 9). The evolution of the axial skeletomuscular system in sauropodomorphs remains a matter of future research.

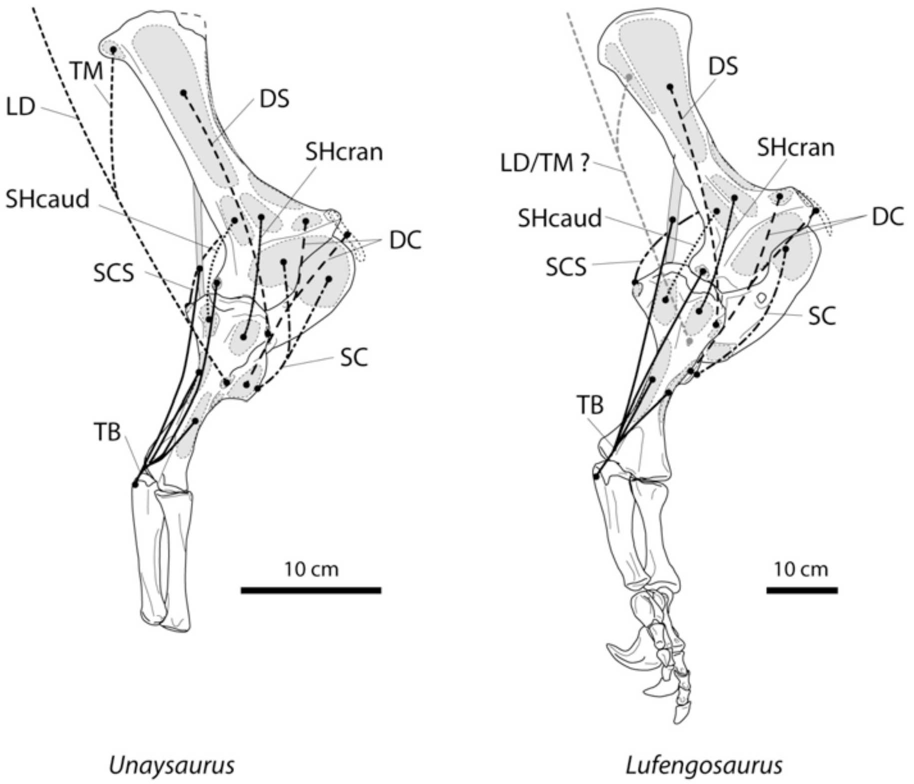

Figure 7-15. Comparison of the pectoral skeletomuscular system of the 'prosauropods' *Unaysaurus* and *Lufengosaurus* in lateral view. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle. For explanations see text.

The skeletomuscular system of the shoulder is relatively uniform in basal sauropodomorphs, including *Antetonitrus* (figs. 7-15, 7-16). Due to slightly different proportions of the scapulocoracoid, the inferred courses of the deltoid and subcoracoscapular muscles vary in their angle relative to a vertical axis through the glenoid, but functional improvements of the plesiomorphic sauropodomorph system (like in *Saturnalia* and *Efraasia*) cannot be inferred from these patterns. Instead, a single skeletomuscular *bauplan* shared by all basal sauropodomorphs was adapted for different purposes by slightly altering the position of essential points of insertion (e.g., the medial tuberosity), or by modifying the form and orientation of the joints (see above).

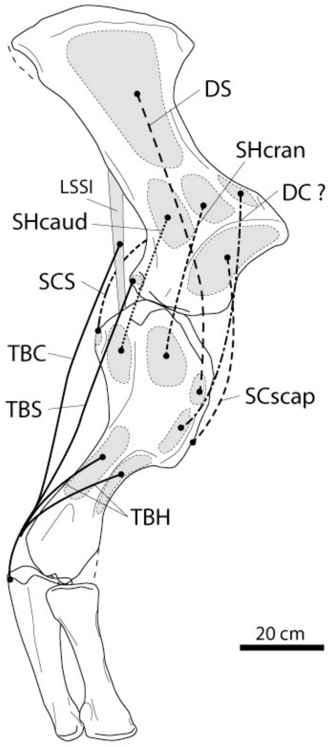

Figure 7-16. Reconstruction of the pectoral skeletomuscular system of *Antetonitrus* in lateral view. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle. For explanations see text.

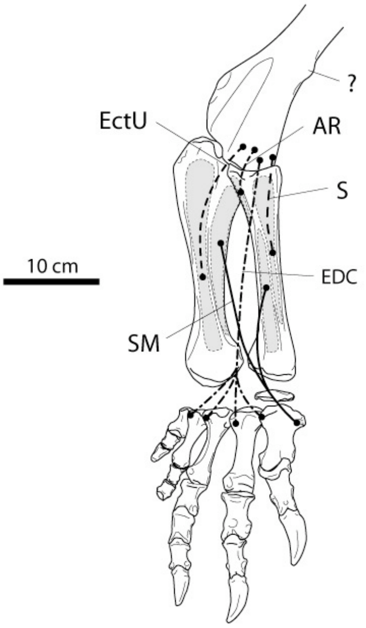

Figure 7-16. Reconstruction of the skeletomuscular system of the cranial side of the antebrachium of *Plateosaurus* in dorsal view. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle. For explanations see text.

In the antebrachium, the courses of many muscles are hard to infer. Their origins, the epicondyles, exhibit no unambiguous osteological correlates, and their plesiomorphic sites of attachment, the proximal carpals, do not ossify in sauropodomorphs. It may be speculated that certain tubercles on the distal expansions of radius and ulna might correlate to modified insertions of the carpal flexors and extensors, but this assumption is hard to test. In general, the courses of inferable forearm muscles are plesiomorphic (fig. 7-16). The robust structure of the antebrachial elements of most ‘prosauropods’ not only indicates increased tolerance against compression (i.e., in support or locomotion), but also provides enlarged muscular attachment sites for the manual supinators (fig. 7-16, M. supinator manus) and pronators, which may have been important both for grasping actions and for locomotion. However, the course of the main manual pronator, M. pronator quadratus, cannot be inferred, since its plesiomorphic point of attachment, the ulnare, is not ossified. The presence of a distinct tubercle cranially on the humeral midshaft in *Plateosaurus* and some other forms is enigmatic. This tubercle obviously indicates the attachment of an unidentified muscle (‘?’ in fig. 7-16), but its position seems too distant from the elbow joint to correlate to one of the ectepicondylar muscles. Possibly, it indicates a modified origin of M. brachialis, or even of M. humeroradialis, if this muscle was retained in basal sauropodomorphs (see chapter 6).

In summary, most of the skeletomuscular system of the forearm and hand of basal sauropodomorphs cannot be reliably reconstructed, due to too many unknowns. Hopefully, a better understanding will be made possible by future research, e.g. by utilizing computer simulations and biomechanical models.

Conclusions

The forelimbs of basal sauropodomorphs retained the skeletomuscular system inherited from the earliest representatives of this group. However, individual taxa show specializations towards improved grasping (e.g., *Plateosaurus*) that prevent efficient quadrupedal locomotion; others adapted for improved quadrupedal locomotion by modifying the form of the hand, and developed advanced capabilities to pronate it. The fact that there are two types of manus pronation systems that seem to be randomly distributed in the current topology of basal sauropodomorph relationships (according to Yates, 2007) possibly reflects our inadequate understanding of the phylogeny of the group. Another plausible explanation is that changes in modes of locomotion (e.g., from facultative to habitual quadrupedalism, or from quadrupedalism to habitual bipedalism and vice versa) occurred independently at several points in basal sauropodomorph evolution. Nevertheless, no basal sauropodomorph, including *Antetonitrus*, exhibits unambiguous adaptations in the skeletomuscular system that might indicate an improved, parasagittal stance and gait of the forelimb. Instead, the plesiomorphic protraction/retraction system (M. pectoralis and M. deltoideus clavicularis acting on the deltopectoral crest) is retained, which inflicts a significant lateral component in the movements of the humerus.

8 Functional morphology of the pectoral girdle and forelimb in basal sauropods

Introduction

The radiation of sauropod dinosaurs began during the Late Triassic, and the group soon reached global distribution. Simultaneously, the body size of sauropods highly increased compared to basal sauropodomorphs, leading to gigantic forms already in the Rhaetian (Buffetaut et al., 2002). Naturally, this increase in size is also reflected in the construction of the limbs, the organs that support the body mass. Soon after the first discoveries of complete sauropod skeletons, it was recognized that sauropods possessed columnar, graviportal extremities (Osborn and Granger, 1901; Riggs, 1901; Hatcher, 1902; Abel, 1910; Holland, 1910; *contra* Hay, 1908, 1910, and Tornier, 1909). In recent years, the understanding of the constructional principles of the sauropod pectoral girdle and forelimb increased significantly by a number of observations in neosauropods (Bonnan, 2001, 2003, 2004; Wilhite, 2003; Schwarz et al., 2007a,b). However, the question of morphological transformations in course of the transition from basal sauropodomorphs to 'true' sauropods has only been initially explored (Bonnan and Yates, 2007). Therefore, this chapter describes in detail the osteology and inferred myology of the pectoral girdle and forelimb of basal sauropods, and provides functional interpretations of these observations. The meaning of these differences from basal sauropodomorphs for the evolution of the sauropod *bauplan* will then be explored in length in chapter 9.

In recent years, new discoveries in Upper Triassic and Lower Jurassic strata in South Africa and East Asia began to fill the morphological gap between typical sauropods and 'prosauropods' (He et al., 1998; Buffetaut et al., 2000; Yates and Kitching, 2003). As a consequence, the definition of the taxonomic unit 'Sauropoda' became a matter of debate. Salgado et al. (1997) proposed a node-based definition of this clade, including *Vulcanodon karibaensis* and more derived sauropodomorphs, while others preferred a stem-based definition, including all sauropodomorphs that are more closely related to *Saltasaurus* than to *Plateosaurus* (Wilson and Sereno, 1998; Sereno, 1999b; Upchurch et al., 2004). According to the latter definition, a number of taxa mentioned in the previous chapter (*Jingshanosaurus*, *Melanorosaurus*, *Antetonitrus*) already belong to Sauropoda. However, the morphological gap between the forelimbs of these forms and those of later sauropods renders a separate treatment of both *baupläne* more convenient. Therefore, the chapter at hand deals with those basal sauropods that already show clear modifications of the skeletomuscular system of the forelimb. The important but incompletely described transitional form *Gongxianosaurus*, which has been briefly mentioned in the previous chapter, will also be addressed for comparative reasons.

Data quality

A look at the temporal and spatial distribution of basal sauropods reveals a major problem for the understanding of the evolution of locomotion in basal sauropods (fig. 8-1). Currently, only few taxa that preserve forelimb elements are known from Lower Jurassic strata. Most of these are incomplete, others are taxonomically or stratigraphically problematic (see below), and again others are currently in description, restricting public access to the material. The first known sauropods with virtually complete skeletons come from the Middle Jurassic of China, an area regarded as largely isolated from the rest of Pangaea during most of the Triassic and Jurassic (see Upchurch, 1995; Golonka, 2007; fig. 8-1). This scarcity of data does not prevent an analysis of morphological transformations, but we should be aware of certain insecurities about interpretations of the early record of sauropod dinosaurs. Hence, future discoveries in the Lower Jurassic will refine (and probably alter) our understanding of the evolution of the sauropod pectoral girdle and forelimb significantly. To get an overview over the reliability of the data analyzed here, short accounts on all relevant taxa will be given in the following.

Gongxianosaurus shibeiensis from the Lower Jurassic Ziliujing Formation of Sichuan, China, has been erected and preliminary described by He et al. (1998), Lou and Wang (1999, 2000), and Lou et al. (1999). He et al. (1998) also provide a sketch of the pectoral girdle and forelimb as found in the field. At least four individuals of *Gongxianosaurus* have been excavated and brought to Yuzhou University, Chongqing, Sichuan (Lou and Wang, 2000), but are currently in preparation for a detailed account on the osteology of this taxon (Li, pers. comm. 2006). *Gongxianosaurus* could not be examined personally during this study, and may therefore only be assessed by means of the brief descriptions and the figure published. Unfortunately, none of the aforementioned works gives an age for this find that is more precise than 'Early Jurassic'. The Ziliujing Formation stratigraphically superposes the prosauropod-bearing Zhenzhuchong Formation (Dong et al., 1983), which has been dated as Toarcian to Bajocian (Wang and Sun, 1983).

Even if the latter estimate were to young, it may be concluded from the stratigraphic succession (Dong et al., 1983) that both formations are younger than the Lower Lufeng Series of Yunnan, which is Sinemurian in age (Luo and Wu, 1994), and probably older than the sauropod-dominated Lower Shaximiao Formation of Sichuan, which is dated as Bathonian (Dong and Tang, 1984). Dong (1984) originally based the age determination of the Ziliujing Formation on the discovery of an isolated dentary that resembles *Lufengosaurus*, but recent discoveries from the Bathonian of Madagascar demonstrate that sauropodomorphs with 'prosauropod'-like teeth still existed in the Middle Jurassic (Buffetaut, 2005). Therefore, it is plausible that the Ziliujing Formation is at least Toarcian in age (rendering the Zhenzhuchong Formation Pliensbachian), and might even be younger.

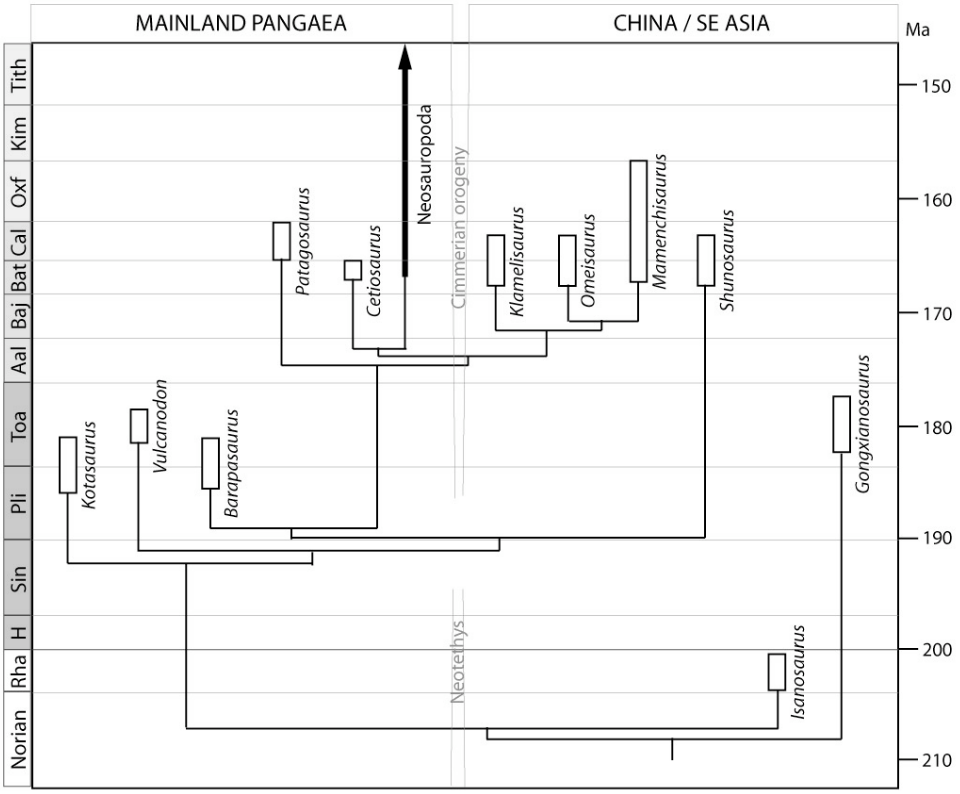

Figure 8-1. Relationships, temporal, and geographical distribution of basal sauropods. Cladogram combined after Upchurch et al. (2007) and Yates (2007). Note that the topology of the basal sauropod tree is still debated, and that neosauropods are also known from the Bathonian of China (*Abrosaurus, Bellusaurus, Daanosaurus*). *Klamelisaurus* has not been incorporated in a cladistic analysis yet, but shows affinities to Mamenchisauridae (Upchurch, 1995; Upchurch et al., 2004).

Isanosaurus attavipachi is based on an assembly of several vertebrae, chevrons, a sternal plate, a right scapula, and a left femur from the Rhaetian Nam Phong

Formation of Thailand (Buffetaut et al., 2000). These authors present drawings of the scapula in lateral view and of the sternal plate in ventral view, but do not describe these elements in detail. Due to the fragmentary nature of the holotype, doubts on the phylogenetic position of *Isanosaurus* remain, and the published figure of the scapula does not show many osteological details. Buffetaut et al. (2002) describe and figure an incomplete sauropod humerus from the same formation and discuss its significance, but this specimen cannot be assigned to *Isanosaurus* since there is no overlap.

Vulcanodon karibaensis comes from a sandstone lens sandwiched between Lower Jurassic lava flows of the terminal Karoo volcanism in northern Zimbabwe, and was described and figured by Raath (1972). The Karoo lava flows had not been dated precisely at that time, leading Raath (1972) to estimate the age of *Vulcanodon* as Hettangian, based on the 'advanced' anatomy of this taxon relative to 'melanorosaurids' (see also Olsen and Galton, 1984). However, recent studies determined the Karoo volcanism to be Toarcian in age, rendering *Vulcanodon* 20 million years younger than previously believed (Duncan et al., 1997; Yates et al., 2004). The semi-articulated holotype material of *Vulcanodon* includes a right ulna, a right radius, and some metacarpals and manual phalanges, all being described and drawn by Raath (1972). Cooper (1984) re-describes and refigures the holotype material plus newly collected specimens from the same locality, including two fragmentary humeri and a fragmentary scapular blade. The *Vulcanodon* material could not be examined personally during this study, due to political instability in Zimbabwe where the specimens are housed. Therefore, the information on *Vulcanodon* given in this chapter is solely based on published accounts.

Barapasaurus tagorei was erected and described by Jain et al. (1975), based on scattered remains that were collected from the Kota Formation of the Godavari Valley, central India. Jain et al. (1975) state that most elements were found isolated in various localities, but some of the material was partly associated. The collected elements, which include a right scapula, a right coracoid, and left and right humeri, were used to mount a skeletal reconstruction in the Indian Statistical Institute in Kolkata. Jain et al. (1975, 1979) give no statement if the scapulocoracoid and the humerus were found associated, or if these elements were found in the vicinity of other postcranial elements. In the same area, P. Yadagiri worked on a bonebed that yielded *Barapasaurus*-like ilia, as well as a second, more plesiomorphic iliac type (Yadagiri et al., 1979). One of these plesiomorphic ilia was published as the holotype of a new genus and species, *Kotasaurus yamanpalliensis*

(Yadagiri, 1988). More material from the bonebed was assembled in form of a skeletal restoration in the B. M. Birla Science Center, Hyderabad, India, with missing parts reconstructed by plaster models. The morphology of this mount was recently described by Yadagiri (2001), however without clearly distinguishing between original fossils and plaster reconstructions. Personal examination of the *Kotasaurus* mount and of additional material from the same locality housed at GSI-SR revealed that at least three sauropod taxa are represented in the Kota Formation, rendering the current compilations of both *Barapasaurus* and *Kotasaurus* highly questionable. Additional to these taxonomical flaws, there are also insecurities about the age of the Kota Formation. Originally claimed to be Liassic, based on a semionotid fish fauna (Jain, 1973, 1996; Bandyopadhyay and Row-Chowdhury, 1996), recent accounts now prefer a Pliensbachian to Aalenian age (Bandyopadhyay, 1999; Bandyopadhyay et al., 2002). However, palynological data possibly indicate a much younger age (G. V. R. Prasad cited in Buffetaut et al., 2000). Under consideration of these taxonomical and stratigraphical uncertainties, the morphology of the forelimb elements assigned to *Barapasaurus* and *Kotasaurus* is shortly introduced in this chapter, but no attempt of a skeletomuscular reconstruction will be made.

Other Early Jurassic sauropods are *Ohmdenosaurus liasicus* from the Toarcian of Germany (Wild, 1978), '*Zizhongosaurus chuanchengensis*' from the ?Toarcian (see above) Ziliujing Formation of Sichuan, China (Dong et al., 1983), and *Tazoudasaurus naimi* from the Toarcian of Morocco (Allain et al., 2004). None of these taxa preserves forelimb elements. Moreover, Barrett (1999) described a sauropod dentary from the Sinemurian Lower Lufeng Series of Yunnan, China. Formerly, this element had been attributed to '*Kunmingosaurus wudingensis'*, a taxon now regarded as a *nomen nudum* (Barrett, 1999).

The situation improves significantly in the Middle Jurassic. A rich dinosaurian fauna is known from the Bathonian Lower Shaximiao Formation of Sichuan, China, and includes the eusauropods *Shunosaurus lii*, *Omeisaurus junghsiensis, O. tianfuensis,* and *Mamenchisaurus (Zigongosaurus) fuxiensis*, the basal macronarians *Abrosaurus dongpoi* and *Daanosaurus zhangi*, and the sauropod incertae sedis *Datousaurus bashanensis*. Several species of *Mamenchisaurus* have also been found in the succeeding Upper Shaximiao and Penglaizhen Formations (e.g., He et al., 1996), which are regarded as Oxfordian (Weishampel et al., 2004b). The forelimb osteology of *Shunosaurus*, *Omeisaurus* and *Mamenchisaurus* is comparatively well described in published accounts (Young, 1939, 1958; Dong et al., 1983; He, 1984;

He et al., 1984, 1988; Zhang et al., 1984, 1998; Zhang, 1988; Pi et al., 1996, 2002; Tang et al., 2001; Ye et al., 2001). However, personal examination of the *Shunosaurus* holotype (IVPP V9065) led to the recognition of fundamental differences in the morphology of the forelimb between the type and the referred, articulated specimens (ZDM 5003, 5006, 5008). The significance of this observation could not be resolved during this study, because the curating institution (ZDM) refused to grant access to most of the Dashanpu material. However, published accounts and the specimens in IVPP and CUT allow for a reasonable assessment of the anatomy of *Omeisaurus* and *Mamenchisaurus*. Regarding *Shunosaurus*, this work refers to the forelimb anatomy of the articulated specimens ZDM 5003 and 5008 as figured by Zhang (1988) and Peng et al. (2005), since these are the only examples of a non-mamenchisaurid basal sauropod that preserve the manus. Pending future taxonomic works, the assignment to *Shunosaurus* is retained provisionally.

Klamelisaurus gobiensis from the Bathonian Wucaiwan Formation of the Junggar Basin, Xinjiang, China, was erected and described by Zhao (1993). It was originally classified as brachiosaurid, but Upchurch (1995) and Upchurch et al. (2004) noted the affinities of this taxon to Mamenchisauridae, which could be confirmed by personal examination. *Klamelisaurus* (IVPP V9492) comprises a well-preserved right forelimb (without manus). Under comparison to the published accounts on *Omeisaurus* and *Mamenchisaurus*, this specimen therefore serves as a model for mamenchisaurid forelimbs in the anatomical descriptions and discussions below.

Another basal sauropod taxon that comprises forelimb elements, *Yuanmousaurus jiangyiensis* from the Middle Jurassic Zhanghe Formation of Yunnan, China, has recently been erected by Lü et al. (2006). The age of the Zhanghe Formation is not entirely clear, but the presence of an advanced ‘prosauropod’ (*Yunnanosaurus youngi*; Lü et al., 2007) in the same strata might indicate a lower Middle Jurassic age. The *Yuanmousaurus* material shows affinities to *Patagosaurus* and seems to be more derived than *Omeisaurus*, but the phylogenetic position of *Yuanmousaurus* remains unclear (Lü et al., 2006). Due to the very recent publication of this taxon, the account on its forelimb anatomy below could only be based on the descriptions and photographs in Lü et al. (2006).

Patagosaurus fariasi from the Callovian Cañodon Asfalto Formation of Cerro Condor, Chubut, Argentina was erected and described by Bonaparte (1979, 1986). The same locality also yielded the basal sauropod *Volkheimeria chubutensis* (which comprises no forelimb material). The *Patagosaurus* material is comparatively well preserved and comprises several scapulae, coracoids, and humeri, plus the complete forelimb (without manus) of a subadult individual (MACN CH-932). However, the *Patagosaurus* hypodigm seems to contain two different taxa (Rauhut, 2003b), and it cannot be demonstrated beyond doubt that MACN CH-932 belongs to the same species as the holotype (PVL 4170). Nevertheless, the specimen will be regarded as *Patagosaurus* in this work, and will serve as the main example for the forelimb anatomy of a basal sauropod (see section 'Anatomy' below).

Finally, *Cetiosaurus oxoniensis* from the Bathonian Forest Marble of Oxfordshire, England is regarded as standing close to the base of the Neosauropoda (Upchurch and Martin, 2002). The OUMNH specimen comprises a complete forelimb (without manus) and a fragmentary sternal plate. After a long and confused taxonomic history, Upchurch and Martin (2003) proposed the best-preserved *C. oxoniensis* specimen from Oxford to serve as a neotype for the genus *Cetiosaurus*, pending a petition to the ICZN. Unfortunately, not all forelimb elements could be examined from all sides during this study, because the scapula, humerus, radius, and ulna are mounted in a showcase at OUMNH.

In summary, it becomes evident that there are currently no Jurassic sauropods known that definitely come from pre-Toarcian strata, with the exception of the dentary from the Lower Lufeng Series (Barrett, 1999). Moreover, the Toarcian taxa that preserve forelimb elements might be significantly younger (*Gongxianosaurus, Barapasaurus, Kotasaurus*), are taxonomically questionable (*Barapasaurus, Kotasaurus*), or are incomplete (*Vulcanodon*). The only definite proof that sauropods with advanced forelimb *bauplans* existed prior to the Toarcian comes from the Rhaetian record of Thailand (Buffetaut et al., 2000, 2002). Consequently, the data on sauropod forelimb evolution exhibits a gap of at least 15 million years. Moreover, good data are currently only available from Bathonian and younger strata, virtually extending the gap to *Antetonitrus* to more than 40 million years (fig. 8-1). The 'leap' in forelimb morphology described in the following sections is therefore an artefact caused by an incomplete fossil record, and does not necessarily reflect a distinct evolutionary event.

Anatomy

As mentioned above, in the following anatomical descriptions *Patagosaurus fariasi* (MACN CH-932) will be used as a standard model for the forelimb anatomy of a basal sauropod. Where necessary, comparisons to other early sauropods will also be incorporated. The forelimb anatomy of mamenchisaurids will be summarized and compared in the second part of this section. Due to the altered, columnar position of the sauropod forelimb, the developmentally ventral face of the humerus is referred to as the cranial side throughout this chapter; the orientations of the remaining surfaces are changed accordingly.

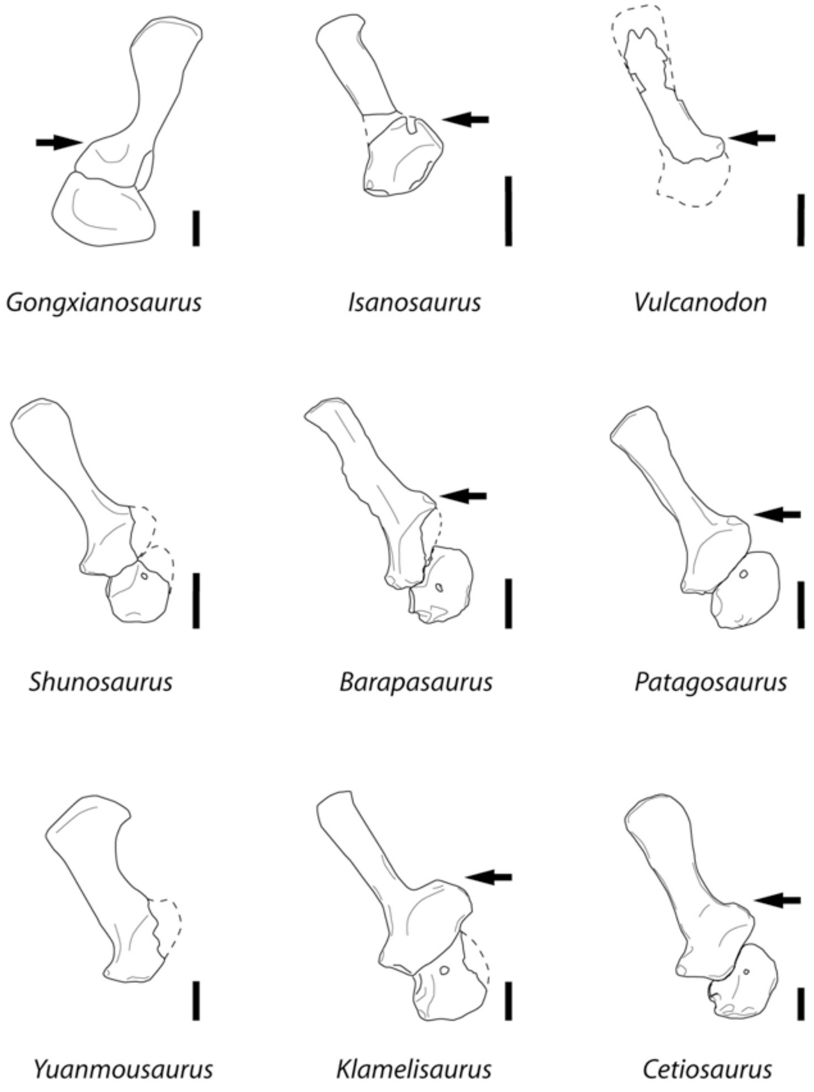

Figure 8-2. Comparison of basal sauropod right scapulocoracoids. Black arrows indicate the clavicular articulation on the acromion. *Gongxianosaurus* is shown in medial view (redrawn after He et al., 1998), all others in lateral view. *Isanosaurus* redrawn after Buffetaut et al. (2000), *Vulcanodon* redrawn after Cooper (1984), *Shunosaurus* redrawn after Zhang (1988), and *Yuanmousaurus* redrawn after Lü et al. (2006). Scale bar = 20 cm.

<u>*Patagosaurus* and other non-mamenchisaurid basal sauropods</u>

Scapulocoracoid. In *Patagosaurus* and most early sauropods, the scapula has a long, slender blade with only a slight distal expansion (figs. 8-2, 8-3). The expansion is somewhat more marked in *Shunosaurus* and *Cetiosaurus*, but distinct in *Gongxianosaurus* and considerably enlarged in *Yuanmousaurus*. The cranial edge of the blade is straight or slightly concave, but distinctly concave in *Cetiosaurus* and *Gongxianosaurus*. With the exception of the latter taxon, the distal edge of the blade is rather straight. A distinct caudal flange protrudes from the caudal edge of the blade. The flange is positioned distal to the proximal third of the blade in *Patagosaurus* and *Barapasaurus*, but proximally placed in *Cetiosaurus*. In *Barapasaurus*, the caudal flange exhibits seemingly pathologic, irregular bone growth that broadens the blade significantly in this area (fig. 8-2). The distal part of the blade is flat laterally, but convex proximally.

On the cranial part of the proximal base of the blade, a narrow, subtriangular depression is found in *Patagosaurus* and *Cetiosaurus*, but is not well marked in other early sauropods. Cranial to the base of the blade, an oval to subtriangular facet on the acromion marks the clavicular articulation. This facet is usually craniolaterally directed. The scapular head, which is significantly deeper than in ‘prosauropods’, is entirely occupied by a large, oval ventrolateral fossa that extends caudoventrally to the glenoid. In *Cetiosaurus*, it extends even further, ending dorsal to the center of the glenoid rim. A distinct acromial ridge borders the ventrolateral fossa dorsally. One of the most marked differences to basal sauropodomorphs pertains to the angle between the long axis of the scapular head and the axis of the blade: usually accounting for 90° or more in ‘prosauropods’, this angle is well below 90° in all sauropods but *Gongxianosaurus*, and reaches only 50° in *Barapasaurus*. Immediately caudodorsal to the glenoid, an oval, caudally directed rugosity is found in all basal sauropods; in *Cetiosaurus,* this structure is more medially directed. On the medial side of scapula, there is an elongate facet proximomedial to the caudal flange of the blade, and an oval fossa cranioproximally on the base of the blade. The distal two thirds of the medial blade are flattened. Both the clavicular articulation and the supraglenoidal rugosity are visible in medial view. Dorsal to the glenoid, the supraglenoidal buttress is robustly developed. The scapulocoracoidal articulation can be observed in *Barapasaurus* only; in this taxon, a peg on the scapula articulates with a socket on the coracoid.

The coracoid of basal sauropods has an oval to subcircular outline, being considerably less craniocaudally elongate than the coracoid of most basal sauropodomorphs. The position of the coracoid foramen varies. The external side of the coracoid is strongly convex but bears no craniocaudal ridge; the internal side is strongly concave. In *Barapasaurus*, the external face is subdivided into three distinct facets, including a craniodorsal, a central, and a ventral facet.

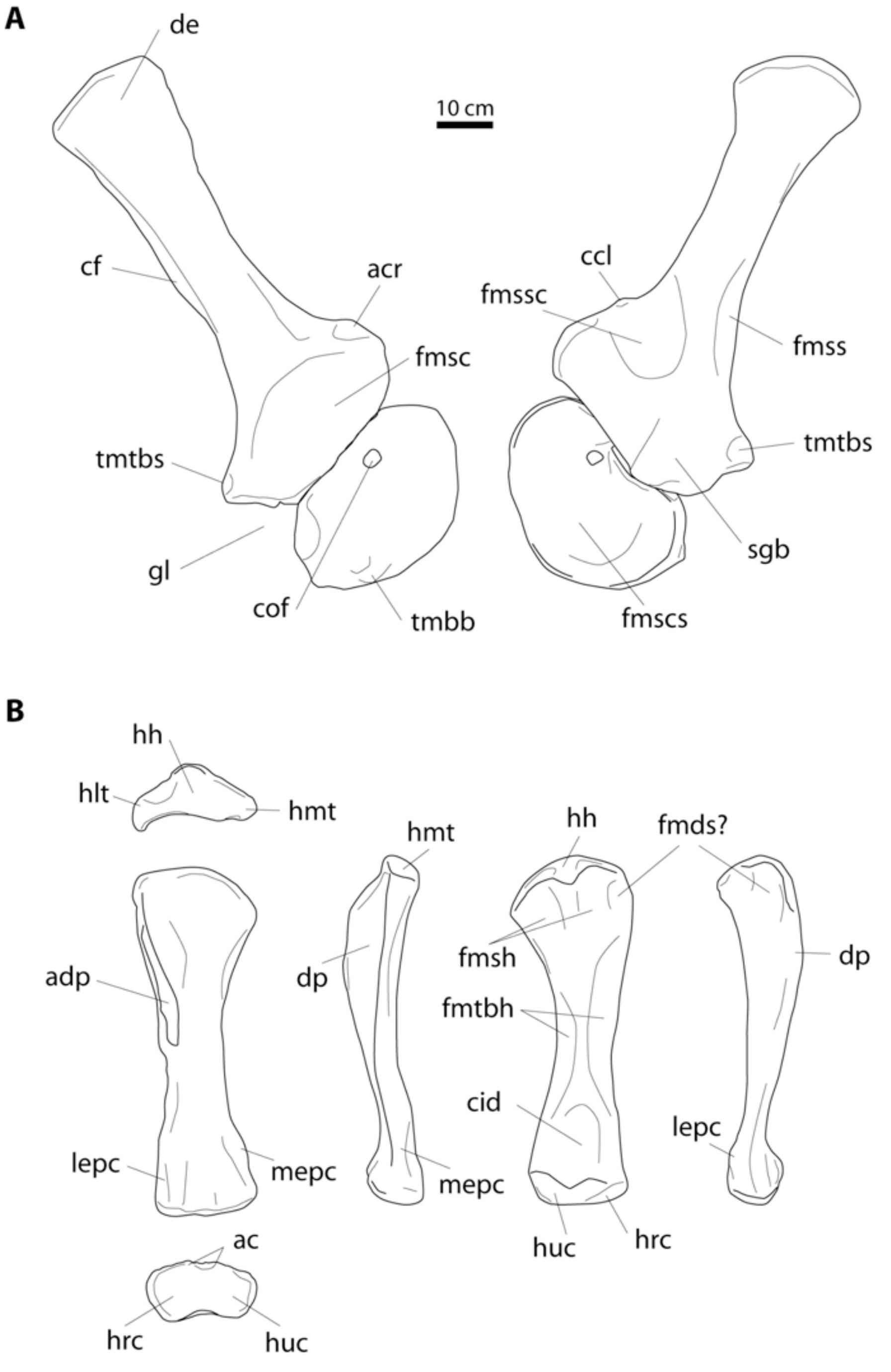

Figure 8-3. Osteological structures of the scapulocoracoid and humerus of *Patagosaurus*. A, right scapulocoracoid in lateral (left) and medial (right) views. B, right humerus in (from left to right) proximal, cranial, distal, medial, caudal, and lateral views.

Ventromedially near the medial edge, a slight eminence marks the attachment of M. biceps brachii. The subglenoid fossa has no lateral border and opens cranially, except in *Barapasaurus* where there is a distinct, transversely rounded ridge lateral to this fossa. The coracoidal part of the glenoid is usually smaller than the scapular part, but equal in size in *Barapasaurus*. The articular surface of the glenoid slightly extends onto the external side of the coracoid. Uniquely in *Barapasaurus*, the medial edge of the coracoid exhibits a 20 mm wide furrow that is bordered externally and internally by deep ridges.

Humerus. In *Patagosaurus*, the humerus is broad transversely but craniocaudally compressed (fig. 8-3). Relative to the width of the shaft, both the proximal and distal ends of the humerus are only slightly expanded. The proximal end is curved, with a concave cranial and convex caudal side. The medial tuberosity is oriented in parallel with the humeral head, instead of being caudally deflected. The ovoid humeral head significantly protrudes over the caudal face of the shaft, rendering the proximal end subtriangular in proximal view. The lateral tubercle is clearly offset from the humeral head, but does not markedly project over the caudal shaft. In cranial view, the humeral head is only slightly vaulted over the level of the medial tuberosity and the base of the deltopectoral crest. The deltopectoral crest is relatively deep (but much less so than in basal sauropodomorphs) and extends over 40% of the length of the humerus. In other basal sauropods, the crest is less prominent and significantly shorter. In these forms, the craniomedially-oriented apex (which is not preserved in MACN CH-932) is distinctly offset from its base, producing a distinct paramarginal groove on the lateral side of the crest. Medial to the crest, a shallow, subtriangular fossa extends over the proximal third of the humerus. In medial view, the humeral shaft is slightly sigmoidal, but the articular surfaces of the proximal and distal ends are parallel. The proximal part of the caudal side of the shaft exhibits two subcircular depressions on both sides of the buttress that supports the humeral head, and a third, smaller facet laterally below the lateral tubercle. Distal to the proximal expansion, the humeral shaft is subdivided into elongate facets laterally and medially; however, the bone surface is not well preserved in MACN CH-932. On the proximal caudolateral edge of the shaft, a prominent ridge borders the lateral side of the deltopectoral crest.

The distal expansion is not as wide as the proximal expansion. Cranially, there is no intercondylar depression. Instead, the distal cranial edge bears a pair of small, cranially projecting tubercles, the accessory condyles (fig. 8-3). The entepicondyle extends over the entire length of the distal expansion, and has the form of a sharp, elevated ridge. The ectepicondyle bears a low ridge with a cranially adjacent, proximodistally elongate facet.

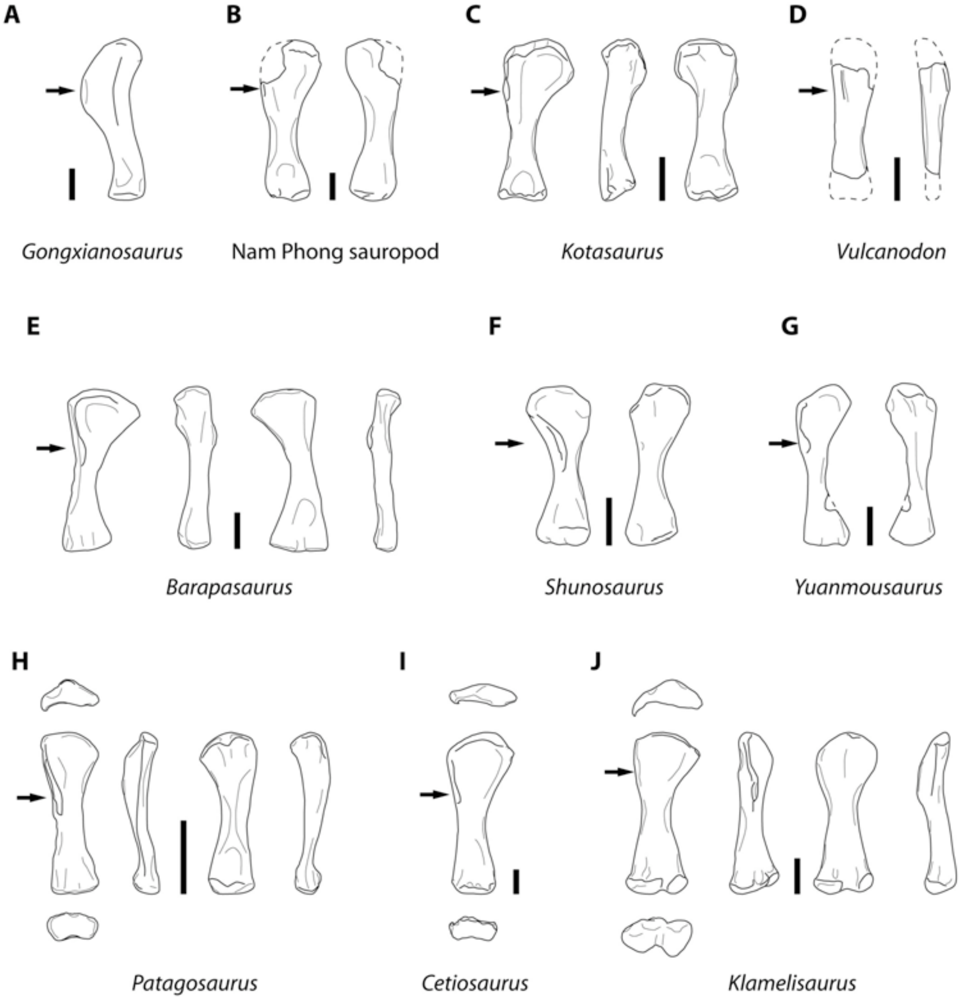

Figure 8-4. Comparison of basal sauropod right humeri. A, *Gongxianosaurus* in medial view (redrawn after He et al., 1998). B, Sauropoda indet. from the Rhaetian Nam Phong Formation of Thailand in cranial (left) and caudal (right) views (redrawn after Buffetaut et al., 2002). C, *Kotasaurus* (BSC unnumbered) in (from left to right) cranial, lateral, and caudal views. D, *Vulcanodon* in cranial (left) and lateral (right) views (redrawn after Cooper, 1984). E, *Barapasaurus* (ISI R 86) in (from left to right) cranial, lateral, caudal, and medial views. F, *Shunosaurus* in cranial (left) and caudal (right) views (redrawn after Zhang, 1988). G, *Yuanmousaurus* in cranial (left) and caudal (right) views (redrawn after Lü et al., 2006). H, *Patagosaurus* (MACN CH-932) in (from left to right) proximal, cranial, distal, lateral, caudal, and medial views. I, *Cetiosaurus* (OUMNH J 13612) in proximal, cranial, and distal views. J, *Klamelisaurus* (IVPP V9492) in (from left to right) proximal, cranial, distal, lateral, caudal, and medial views. Black arrows mark the apex of the deltopectoral crest. Scale bar = 20 cm.

In distal view, the edges of the humeral condyles form a cranially open V, with the radial tubercle being craniolaterally, and the ulnar condyle being craniomedially oriented. Both condyles extend proximally onto the caudal side of the shaft.

Proximal to the condyles, the caudal side of the distal expansion exhibits a shallow but large intercondylar depression. The transverse axes of the proximal and distal expansions are subparallel, since there is no distinct torsion in the humeral shaft.

Other basal sauropods differ in several characters (fig. 8-4). *Gongxianosaurus* and *Kotasaurus* lack a craniocaudal compression of the humeral shaft. In *Gongxianosaurus*, the deltopectoral crest is large and extends almost over 50% of the length of the humerus. Moreover, the humeral shaft is distinctly sigmoidal in this form. In *Shunosaurus, Cetiosaurus, Kotasaurus,* and *Barapasaurus,* the humeral head is vaulted over the level of the lateral condyle and medial tuberosity (but less prominent in the latter taxon). This character is considerably pronounced in *Yuanmousarus*, which also has an extremely slender humeral shaft (Lü et al., 2006). In *Cetiosaurus* and *Barapasaurus*, the humeral head protrudes over the cranial side of the shaft. The medial tuberosity extends far medially in *Kotasaurus* and *Barapasaurus*, rendering the proximal expansion wider than the distal expansion, and the medial side of the shaft proximodistally strongly concave. *Shunosaurus* is unusual in having a concave lateral edge of the shaft that is even more strongly curved than the medial edge (Zhang, 1988:fig. 46). In *Kotasaurus* and *Cetiosaurus*, the distal expansion is slightly cranially deflected, and lacks a distinct entepicondyle. The latter character is also missing in *Barapasaurus*. *Kotasaurus* has a distinct cranial intercondylar depression caudally, but no accessory condyles cranially. Finally, *Cetiosaurus* lacks an extension of the humeral head onto the caudal side of the shaft.

Antebrachium. In *Patagosaurus* and most other basal sauropods, radius and ulna are slender bones (fig. 8-5). Relative to the length of the humerus, the antebrachium is slightly elongate (see Mauersberger, 2005). The proximal end of the ulna is triradiate: the lateral process is enlarged and almost equals the cranial process in size. Both processes enclose an angle of about 100°. The cranial process has rotated medially relative to the central axis of the olecranon process, rendering the medial edge of the proximal end distinctly sigmoid in proximal view. Moreover, its proximal surface bears no distinct humeral cotyle.

Like in most sauropodomorphs, the ulna lacks an ossified, proximally projecting olecranon process on its caudal side. Instead, the caudal part of the proximal end exhibits a circular, pitted dome that served as the base for the unossified epiphysis (see Discussion below). Proximally on the medial side of the shaft, an elongate oval fossa extends distally for one third of the length of the shaft. This fossa is restricted to the caudal two thirds of the width of the shaft, unlike the condition found in basal sauropodomorphs where it occupies the entire medial side. Distal to this fossa, an elongate facet extends distocranially, followed by another facet distally. An obliquely oriented, rounded ridge separates both facets from each other.

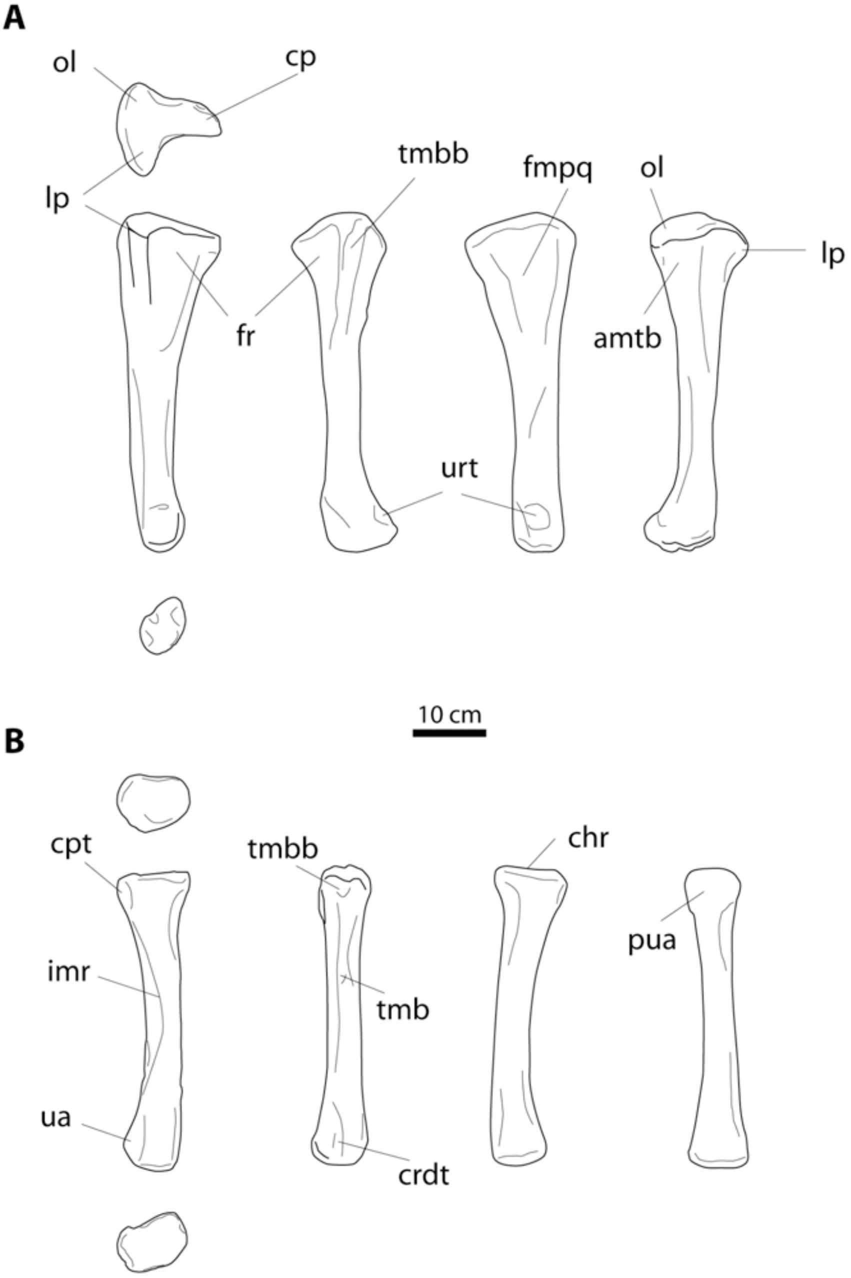

Figure 8-5. Osteological structures on ulna and radius of *Patagosaurus*. A, right ulna in (from left to right) proximal, lateral, distal, cranial, medial, and caudal views. B, right radius in corresponding views.

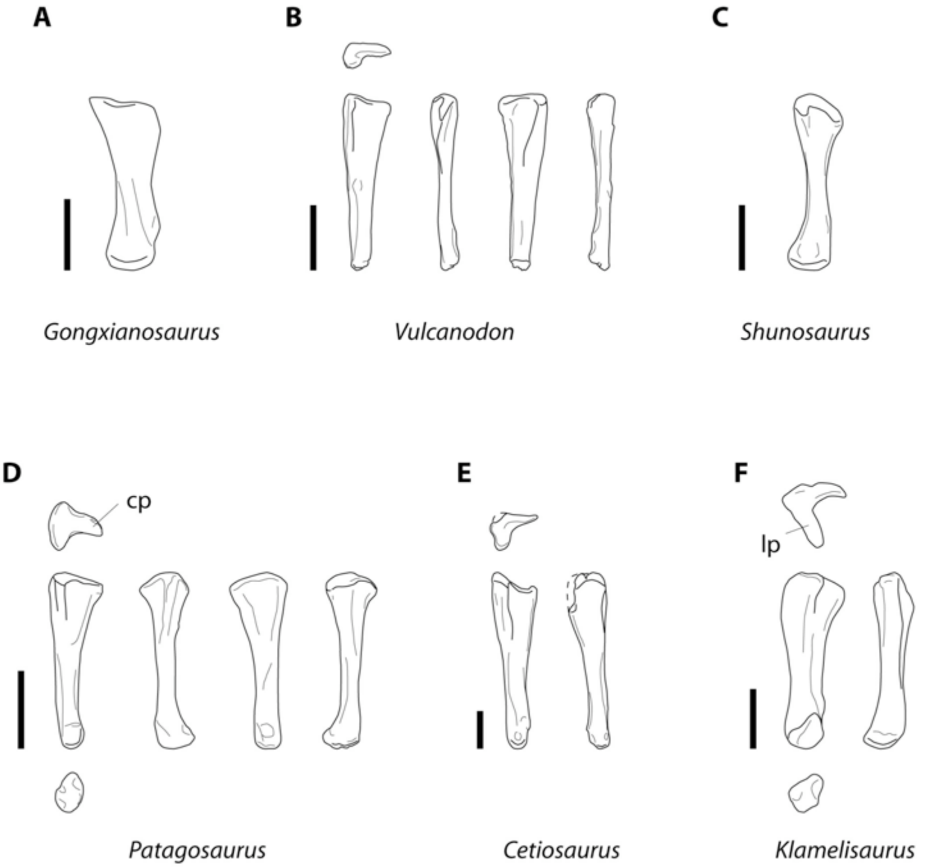

Figure 8-6. Comparison of basal sauropod right ulnae. A, *Gongxianosaurus* in medial view (redrawn after He et al., 1998). B, *Vulcanodon* in (from left to right) proximal, lateral, cranial, medial, and caudal views (redrawn after Cooper, 1984). C, *Shunosaurus* in lateral view (redrawn after Zhang, 1988). D, *Patagosaurus* (MACN CH-932) in (from left to right) proximal, lateral, distal, cranial, medial, and caudal views. E, *Cetiosaurus* (OUMNH J 13611) in proximal (top), lateral (left), and caudal (right) views. F, *Klamelisaurus* (IVPP V9492) in proximal (top), lateral (left), distal (bottom), and cranial (right) views. Scale bar = 20 cm.

The proximal third of the cranial side of the shaft is narrow. Immediately distal to the cranial process, a spindle-shaped tubercle is slightly offset from the cranial edge. The lateral side of the shaft bears a deep, triangular radial fossa with conspicuous longitudinal striations. Caudal to this fossa, the lateral process is supported by a short but robust buttress. An elongate facet extends distally over almost the entire length of the shaft. The caudal side of the shaft is thickened and transversely convex in its proximal part, where it exhibits strong longitudinal striations. The distal end of the ulna is expanded craniomedially, forming a triangular process in distal view. On the craniomedial side of the distal end, a large, oval rugosity marks the radial articulation.

The radius is straight, with its caudal edge being only slightly concave in proximodistal direction. In proximal view, the proximal end is suboval with a straight medial edge, and has no distinct caudoproximal process. Moreover, there is no cotyle for the humerus, but an even, pitted surface. Immediately distal to the proximal articular surface, a subcircular tubercle projects cranially. A similar tubercle is found on the caudolateral edge of the proximal articular surface. Distal to the proximal third on the cranial edge of the shaft, the cranial tubercle has the form of a large, rugose swelling. Starting from the caudoproximal corner of the lateral side, a prominent intermuscular ridge runs craniodistally to the middle of the shaft, then curves caudodistally and ends shortly above the caudodistal corner of the distal expansion. The remaining sides of the shaft are subdivided into elongate, proximodistally oriented facets. The distal end bears a prominent swelling caudomedially, indicating the contact to the ulna, and a rough pitted tubercle cranially.

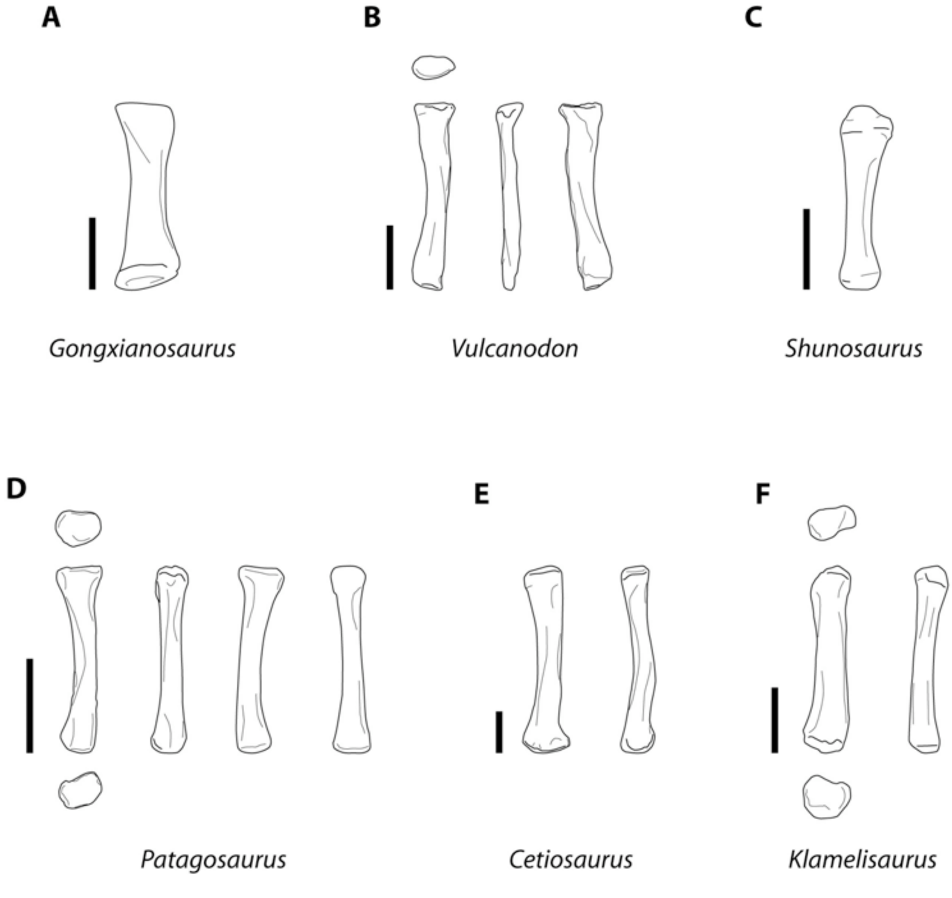

Figure 8-7. Comparison of basal sauropod right radii. A, *Gongxianosaurus* in medial view (redrawn after He et al., 1998). B, *Vulcanodon* in (from left to right) proximal, lateral, cranial, and medial views (redrawn after Cooper, 1984). C, *Shunosaurus* in lateral view (redrawn after Zhang, 1988). D, *Patagosaurus* (MACN CH-932) in (from left to right) proximal, lateral, distal, cranial, medial, and caudal views. E, *Cetiosaurus* (OUMNH J 13611) in lateral (left), and caudal (right) views. F, *Klamelisaurus* (IVPP V9492) in proximal (top), lateral (left), distal (bottom), and cranial (right) views. Scale bar = 20 cm.

The antebrachial elements of other basal sauropods are very similar, with the exception of *Gongxianosaurus* (figs. 8-6, 8-7). In this taxon, radius and ulna are very stout and robustly developed. However, the published descriptions give no further details on these elements. In *Vulcanodon*, the lateral process of the ulna is short and rounded in proximal view, while the cranial process is elongate and slender. In *Cetiosaurus*, both processes are elongate, but the cranial process is longer and transversely narrow.

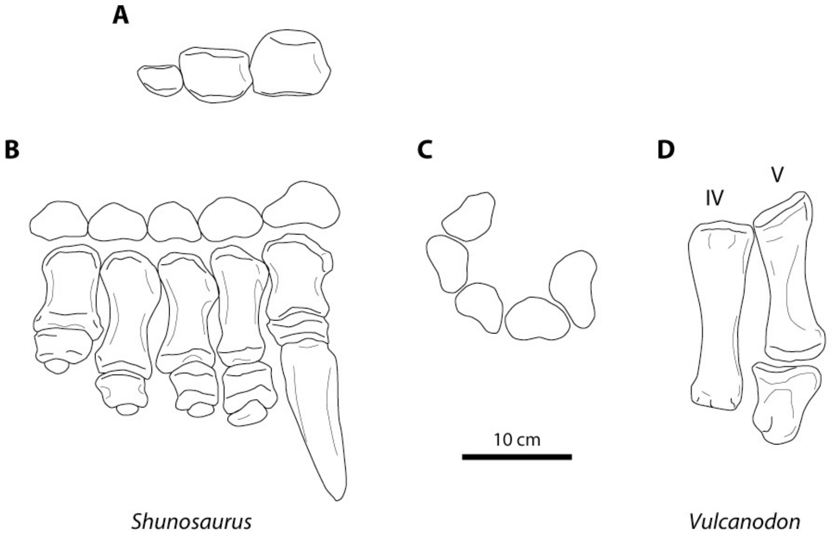

Figure 8-8. Hands of basal sauropods. A, right distal carpals of *Shunosaurus* in dorsocranial view. B, right manus of *Shunosaurus* in dorsal view, with outlines of the metacarpals in proximal view. C, alternate arrangement of the right metacarpus of *Shunosaurus* in proximal view. D, left metacarpals IV and V, plus phalanx V.1 of *Vulcanodon*. A and B, redrawn after Zhang (1988); C, modified from Zhang (1988). D, redrawn after Raath (1972).

Manus. In the course of this study, no manus of a basal sauropod could be examined personally. The only complete hand known was found articulated in a specimen of *Shunosaurus* (present catalogue number: ZDM 5003; see Peng et al., 2005), which was figured and described by Zhang (1988). Zhang (1988:fig. 49) arranged the metacarpals very broad in his reconstruction, rendering the manus 300 mm wide in transverse direction (fig. 8-8B). However, according to the figures in Zhang (1988), the width of the distal ends of radius and ulna in articulation must have been around 150 mm. This discrepancy in width between antebrachium and manus is unnatural: Upchurch (1994, 1998) recognized that the metacarpus probably articulated in a semitubular arrangement, resembling the neosauropod condition, and matching the size of the antebrachium (fig. 8-8C). As reconstructed here, the metacarpal arc of *Shunosaurus* extends over an circle segment of about 200°, and is therefore similar to that of the contemporaneous basal neosauropod *Atlasaurus* (Monbaron et al., 1999). A metacarpal arc has also been described for *Ferganasaurus*, but the metacarpals of this likewise contemporaneous form are arranged in a circular segment of only about 90° (Alifanov and Averianov, 2003). Nevertheless, sauropod tracks with semitubular hands are known already from the Lower Jurassic (Upchurch, 1994; Gierlinski, 1997; Wilson, 2005).

Zhang (1988) specified the manual phalangeal formula of *Shunosaurus* as 2-2-2-2-?2, but Upchurch (1998, 1999) coded it as 2-2-2-2-1. Moreover, Upchurch et al. (2004) depicted the manus with a phalangeal formula of 2-2-2-2-?0 in a modified version of Zhang's (1988) original figure. Peng et al. (2005:fig. 55) presented a novel reconstruction of the manus of a second specimen of *Shunosaurus* (ZDM 5008), showing a phalangeal formula of 2-3-2-2-1, but noted a phalangeal formula of 2-2-2-2-?2 in the diagnosis of this genus.

Irrespective of these uncertainties about the correct reconstruction of the manus of *Shunosaurus*, the published accounts allow for a brief assessment of its osteology. Zhang (1988) recognized three distal carpals, but other specimens have four carpals ossified (Peng et al., 2005). The block-like carpals cap the metacarpals and become successively smaller towards the lateral side of the hand (fig. 8-8A). The metacarpals are robust and lack extensor or ligament pits. Metacarpal I is significantly longer than wide and has slightly asymmetric distal condyles. In proximal view, it is triradiate with slightly concave cranial and lateral edges, instead of 'keyhole-shaped' as in many basal sauropodomorphs. In proximal view, metacarpals II–V are all subtriangular, and have concave cranial rims. Metacarpals II–IV are equal in length; metacarpal V is slightly longer than metacarpal I. The proximal phalanges are block-like, being about as long as wide. Phalanx I.1 is proximodistally compressed, rendering its shape disk-like. The first ungual is strongly enlarged, and almost doubles the first metacarpal in length. On digit II, a vestigial ungual is retained, while the remaining digits exhibit knob-like second phalanges.

In comparison, the preserved metacarpals of *Vulcanodon* are rather slender (fig. 8-8D). They have about the same proximal width as the corresponding elements in *Shunosaurus*, but are about 50% longer. The distal ends exhibit no differentiation into separate condyles; instead, the distal articular surface is reel-like in metacarpal IV and ovoid in metacarpal V (Raath, 1972). Like in *Shunosaurus*, there are no extensor or ligament pits. The subtriangular first phalanx of digit V is robust and ends in a blunt tip (Raath, 1972). Therefore, a possible second phalanx of this digit could only have been vestigial in nature. Judging from the drawings of these elements alone, it is impossible to reconstruct the structure of the entire manus.

Mamenchisauridae

The forelimb anatomy of the mamenchisaurids *Klamelisaurus, Omeisaurus*, and *Mamenchisaurus* differs from other basal sauropods in a number of specializations. In the following, these will be shortly summarized. For comparison, the pectoral girdle and forelimb elements of *Klamelisaurus* are shown in figs. 8-2, 8-4, 8-6, and 8-7.

Scapulocoracoid. Mamenchisaurids have a slender scapular blade and a considerably enlarged scapular head. The angle between the dorsal border of the acromion and the long axis of the scapular blade is less than 90°. Caudodorsal to the clavicular articular facet, a conspicuous triangular process projects dorsally. The coracoid is much reduced relative to the size of the enlarged scapular head: In *Omeisaurus* and *Mamenchisaurus*, the scapular head has almost double the size of the coracoid. In some specimens, the ventrolateral fossa on the scapular head exhibits a slight differentiation into a deeper caudodorsal and a flattened cranioventral part. The scapular part of the widely open glenoid is ventrally and slightly medially oriented, while the coracoidal part extends far onto the external surface of this element. In *Mamenchisaurus*, a channel-like groove runs from the scapular part of the coracoid in craniodorsal direction. The coracoidal part of the glenoid is dorsoventrally enlarged, leading to a reduction of the subglenoid fossa. A long, slender clavicle with a flattened, triangular proximal end has been reported for *Omeisaurus tianfuensis* (He et al., 1988:fig. 43).

Humerus. Mamenchisaurid humeri exhibit a marked medial expansion of the medial tuberosity. The lateral part of the proximal end is elongate but craniocaudally slender. The cranial side of the humeral head extends craniodistally, forming an articular surface for the elongate coracoidal part of the glenoid. The deltopectoral crest is short, the apex ending after about 35% of the length of the humerus. In *Klamelisaurus* and *M. guangyuanensis*, a large, pitted tubercle is situated caudally to the proximal part of the apex. The distal end of the humerus is twisted craniolaterally at about 25° relative to the proximal end.

The distal articular end of the humerus exhibits a complex morphology. In *Klamelisaurus* and *O. tianfuensis,* the epiphyses are almost fully ossified. The radial condyle is larger than the ulnar condyle, both being separated from each other by a distinct constriction. The long axis of the radial condyle stands perpendicular to the long axis of the ulnar condyle, and forms an angle of about 45° with the distocranial edge of the humerus. The accessory condyles are strongly enlarged. In *Omeisaurus* and *Klamelisaurus,* the medial accessory condyle is cone-shaped and projects craniolaterally almost in parallel to the long axis of the radial condyle, while *Mamenchisaurus* has two equally sized, triangular accessory condyles that project cranially and only slightly laterally.

Antebrachium. The radius of mamenchisaurids is similar to that of other basal sauropods, but exhibits a distinct, elongate caudodistal tubercle that serves for articulation with the ulna. In *Klamelisaurus* and *M. constructus*, the ulna is much more robustly build than in most other sauropods but *Gongxianosaurus*. However, the same element is slender in *Omeisaurus* and *M. youngi*. In all mamenchisaurids, the cranial and lateral processes of the proximal end of the ulna are strongly elongate. Standing perpendicular or in a slightly lower angle to each other, they form a distinct 'L' in proximal view.

Manus. Elements of the hands are preserved in *O. tianfuensis* and *M. youngi*. Judging from the published descriptions and figures, the structure of the manus of *Omeisaurus* is similar to *Shunosaurus*, but the metacarpals are significantly more slender and elongate (He et al., 1988). In *Mamenchisaurus*, metacarpals II–V bear triangular facets medially that allow for a tight, semitubular articulation of the metacarpus (Pi et al., 2002). *M. youngi* preserves a large, disk-like distal carpal that caps metacarpals I and II, and another small distal carpal situated proximal to the caudal corners of metacarpals III and IV (Pi et al., 2002).

Muscle reconstructions

Owing to the insufficient taxonomical consistency of most basal sauropod taxa, muscle reconstructions are only attempted for *Patagosaurus* (MACN CH-932). Since the structure of the pectoral girdle and forelimb is relatively similar in many basal sauropods, a comparable muscle system may be expected for these taxa, too. Mamenchisaurids are an exception, since this group shows many specializations of the scapulocoracoid and humerus. These osteological modifications are probably in part related to muscle reconfigurations. A possible functional explanation for these characteristics will be given in the 'Discussion' section below.

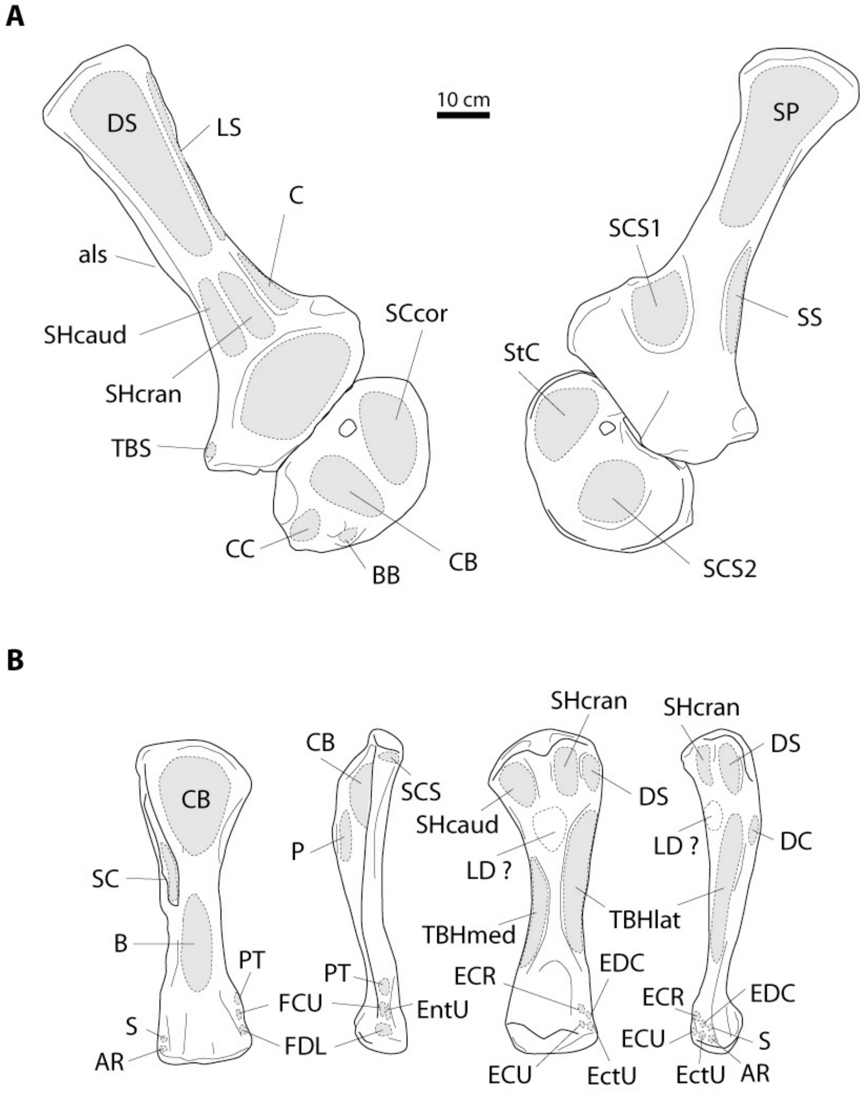

Figure 8-9. Reconstructions of muscle attachment sites on the scapulocoracoid (A) and humerus (B) of *Patagosaurus*. A, scapulocoracoid in lateral (left) and medial (right) views. B, humerus in (from left to right) cranial, medial, caudal, and lateral views. For explanations see text.

Scapulocoracoid. In comparison to basal sauropodomorphs, the pattern of muscle attachments on the scapulocoracoid of *Patagosaurus* appears relatively plesiomorphic (fig. 8-9A). The flattened distal part of the scapular blade probably beared the origin of M. deltoideus scapularis, like in all archosaurs plesiomorphically (chapter 3). M. teres major is not reconstructed here, since the lateral face of the scapular blade lacks a clear differentiation into a cranial and a caudal facet, and the insertion of this muscle on the humerus cannot be delimited. However, these observations do not rule out the presence of this muscle in the living animal. The elongate subtriangular depression at the cranial base of the blade probably correlates to the insertion of M. cucullaris, as inferred for basal dinosauriforms and most basal dinosaurs (chapters 4–7). Dorsal to this facet, M. levator scapulae might have attached to the sharp cranial edge of the scapular blade. In *Patagosaurus*, the caudal flange on the blade might indicate the attachment of a Ligamentum sternoscapulare internum, but owing to the alternate configuration of the coracoid, the course of such a ligament is hard to infer (see Discussion below). Proximally, the convex base of the blade probably provided room for the attachment of Mm. scapulohumerales. Like in all basal archosaurs, the large ventrolateral fossa on the scapular head served for the origin of M. supracoracoideus pars scapularis, while the prominent tubercle caudodorsal to the glenoid correlates to the origin of M. triceps brachii caput scapulare (chapters 3–7). On the medial side of the scapula, the distinct elongate facet medial to the caudal flange indicates the attachment of M. serratus superficialis, like in basal dinosaurs and most basal sauropodomorphs. The depression cranially on the medial side of the base of the blade probably correlates to the origin of M. subscapularis; hence, this muscle remains in the plesiomorphic sauropodomorph position (chapter 6). Like in all basal archosaurs, M. serratus profundus probably attached to the flattened distal part of the medial side of the blade (chapters 4–7).

On the coracoid, muscle attachment sites are hard to delimit. Due to the rather plesiomorphic form of the coracoid, the inferred origins and insertions follow a plesiomorphic pattern. Accordingly, the external side of the coracoid bears the origins of M. supracoracoideus pars coracoidalis cranially, the origin of M. coracobrachialis caudal to the coracoid foramen, and the relatively small insertion of M. costocoracoideus ventral to the glenoid. The indifferent, roughened swelling cranioventral to the glenoid indicates the origin of M. biceps brachii. On the medial side of the coracoid, there are no distinct facets that delimit muscle attachments, but striations indicate that muscles connected to the bone cranially and caudally. Following the plesiomorphic pattern, these are probably M. sternocoracoideus and M. subcoracoideus, respectively.

Humerus. As for the scapulocoracoid, the inferred pattern of muscle attachment sites on the humerus of *Patagosaurus* is rather plesiomorphic (fig. 8-9B). The lateral tubercle, and possibly also the swelling distal to this tubercle, may correlate to the insertion of M. deltoideus scapularis. Like in all archosaurs, the medial tuberosity indicates the attachment of M. subcoracoscapularis. On the cranial side of the shaft, the proximal depression correlates to the insertion of M. coracobrachialis. Following the plesiomorphic pattern, M. pectoralis inserted medially, M. supracoracoideus cranially, and M. deltoideus clavicularis laterally on the deltopectoral crest (as mentioned in chapter 2, these orientations are conventions:

actually, the 'cranial' side of the shaft was craniomedially directed, rendering the attachment for M. pectoralis on the deltopectoral crest caudomedially oriented. See Bonnan, 2003, and Discussion below). Distal to the deltopectoral crest, the wide central part of the shaft provides room for the attachment of M. brachialis. On the caudal face of the humerus, the oval fossae on both sides of the caudally projecting humeral head probably indicate the insertions of Mm. scapulohumerales, like in all basal archosaurs (chapters 4–7). Since there is no distinct scar on the caudal side of the shaft that might correlate to the insertion of a M. latissimus dorsi tendon, this muscle either was lost or had a fleshy insertion. Such a fleshy insertion of M. latissimus dorsi would have been situated distal to the attachments of Mm. scapulohumerales, and proximally between the origins of Mm. triceps brachii capiti humerales. The caudomedial and caudolateral facets of the humeral shaft probably indicate the origins of these latter muscles. The distinct caudolateral tubercle found in some mamenchisaurids is similar in position to the M. latissimus dorsi scar of many 'prosauropods', but considerably larger. Alternative explanations are that this tubercle correlates to a distally shifted insertion of M. deltoideus scapularis, or to a specialized part of M. deltoideus clavicularis (see Discussion below). As for all dinosaurs, the exact configuration of the origins of the epicondylar muscles cannot be inferred reliably, but in most cases this uncertainty does not have much effect on the reconstructed lines of action. The elongate entepicondyle in *Patagosaurus* may indicate a more proximal placement of the origin of M. pronator teres, but this inference is rather speculative, especially since most other basal sauropods lack this distinct shape of the entepicondyle.

Antebrachium. The ulna of *Patagosaurus* (fig. 8-10A) and other early sauropods is characterized by a relatively small proximomedial fossa, probably indicating a reduced origin of M. pronator quadratus. In the living animal, the radial fossa proximal on the lateral side of the ulna was largely filled with the proximal head of the radius (chapter 9), leaving not much room for muscles. Therefore, striations found in this area might correlate to radioulnar ligaments. The tubercle distal to the cranial process probably served for the insertion of the M. brachialis / M. biceps brachii system, like in most diapsids (but see Discussion below). Owing to the position of the radius, the origin of M. supinator manus is reconstructed here as somewhat distal to the proximal end of the ulna. The striated eminence on the caudal side of the shaft indicates the attachment of the M. triceps brachii system. The obliquely craniodistally oriented facets on the shaft correlate to the insertions of M. ectepicondylo-ulnaris laterally, M. entepicondylo-ulnaris caudomedially, and the ulnar head of M. flexor digitorum longus craniodistomedially, following largely the plesiomorphic pattern.

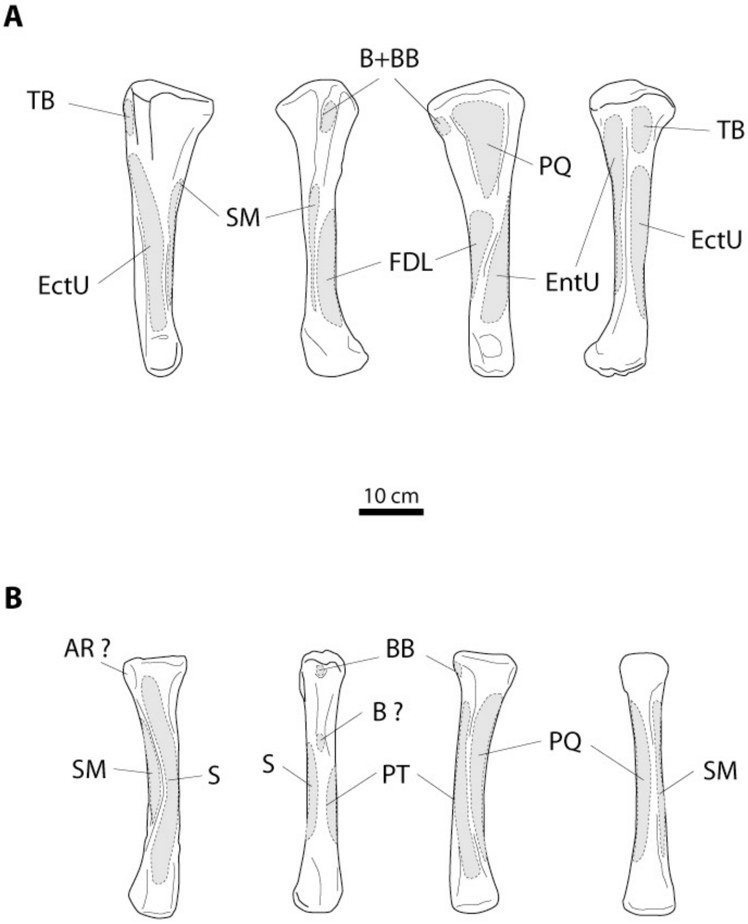

Figure 8-10. Reconstructions of the muscular attachments on the ulna (A) and radius (B) of *Patagosaurus*. From left to right, lateral, cranial, medial, and caudal views. For explanations see text.

As for the ulna, the pattern of muscle attachment sites on the radius differs from that of other archosaurs primarily in the course of these attachments on the shaft, which appears somewhat twisted. Nevertheless, the pattern is rather plesiomorphic: Most muscles are inferred to have attached to the elongate facets that extend almost over the entire length of the shaft, with M. supinator craniolaterally, M. supinator manus caudolaterally, M. pronator quadratus caudomedially, and M. pronator teres craniomedially. The slight eminence on the cranial edge, distal to the proximal third of the bone, is homologous to the cranial tubercle of other early dinosaurs and might therefore have served for the attachment of the M. biceps brachii / M. brachialis system or of M. brachialis alone (see chapters 5–7 and Discussion below). The cranioproximal tubercle immediately distal to the cranial process probably correlates to the insertion of M. biceps brachii, just as the corresponding tubercle on the ulna. Since there is no distinct facet for M. abductor radialis caudoproximally on the lateral side of the radius, this muscle seems to have been reduced or lost. The tubercle on the cranial side of the distal end of the radius might indicate the insertion of M. extensor carpi radialis, which possibly shifted from the unossified radiale onto the radius, but there is no way to test this assumption.

Discussion

Compared to basal sauropodomorphs, sauropods exhibit a number of modifications in all regions of the forelimb. However, the most significant changes occur in the ventral shoulder girdle including the muscles that move the shoulder joint, in the elbow joint, and in the manus.

Osteology and *bauplan*

Scapulocoracoid. The most striking transformation in the shoulder girdle is the reorientation of the scapular head relative to the blade, as indicated by the low angle enclosed by their long axes, and by the wide angle between the supraglenoidal rim and the caudal edge of the blade. Most other modifications of the pectoral girdle are related to this key innovation, as will be shown in the following.

During locomotion, the shoulder joint has to divert ground reaction forces onto the pectoral girdle, which transfers these forces via the Mm. serrati and the dorsal ribs to the vertebral column (Hildebrand and Goslow, 2001). To avoid dislocation and shear stresses that would require additional muscular force to compensate, a vertical orientation of the limbs is most effective for large animals (Gregory, 1912; Gray, 1944; Biewener, 1989a,b, 1990, 1991). The force-diverting joint should be primarily strengthened in line with the vector of the ground reaction force, to compensate for compressive stress. This is one reason why it is most probable that the scapular part of the glenoid was directly ventrally oriented in sauropods, bringing the robust medial supraglenoidal buttress in line with the vertical limb. Other factors support this reconstruction, including the necessity of maintaining both the costosternal and sternocoracoidal articulations, realistic lines of actions of the musculature (e.g., placing the protracting muscles in front of the shoulder joint, not above), and an effective transfer of forces to the Mm. serrati without exerting large torsional forces on the scapular neck. A horizontal orientation of the scapular blade, as often assumed for sauropods (e.g., as depicted in the recent review by Upchurch et al., 2004), is therefore rejected (see chapter 9). With these factors as constraints for the orientation of the scapulocoracoid, it becomes evident that the angle of the scapular blade remained at about 60° relative to the horizontal, as is plesiomorphic for archosaurs (chapter 4). The modified angle between the blade and the scapular head therefore relates to a dorsocranial rotation of the ventral girdle, bringing the coracoids in front of the torso (fig. 8-11). The significance of this modification for the muscular system will be discussed below (section 'Myology'), but several other osteological novelties are causally connected to this alternate position of the coracoid. First, the craniocaudal length of the coracoid is reduced relative to that of the scapular head, rendering the element subcircular in form. This keeps the cranial edge of the bone below the medial articulation of the clavicles, avoiding interference and allowing for a normal (instead of subhorizontal) orientation of the clavicles. Second, and most importantly, the position of the coracoidal portion of the glenoid is no longer ventromedial to the scapular portion, like in basal sauropodomorphs. This renders the glenoid directly ventrally, instead of caudolaterally oriented, and is therefore a crucial modification for a vertical orientation of the humerus. As a consequence, the coracoidal part of the glenoid receives less compressional forces from the humerus, leading to a reduction of its size relative to that of the scapular portion. Moreover, the reorientation of the glenoid allows the humerus to swing in a near-parasagittal plane (rotating its developmentally ventral side cranially), but it can hardly be protracted far beyond the vertical (fig. 8-11). The extension of the glenoid onto the external surface of the coracoid in mamenchisaurids represents a special modification related to this problem, but will be discussed below together with the pectoral muscle system of these animals.

The reduction of the distal expansion of the scapular blade in most sauropods is not easy to explain. The distal expansion forms the base for the suprascapular cartilage, the presence of which is indicated by the wrinkled surface texture of the distal edge. An expanded distal end may correlate to an enlarged suprascapular cartilage, but this assumption cannot be tested. If it were true, differently sized suprascapular cartilages may reflect differential developments of M. rhomboideus, a stabilizing cingulo-axial muscle that plesiomorphically inserts onto the medial side of the suprascapula (chapter 3). However, the extent and physiological cross-section of M. rhomboideus (and therefore its significance for the pectoral skeletomuscular system) cannot be inferred (chapter 3), rendering any further interpretations purely speculative.

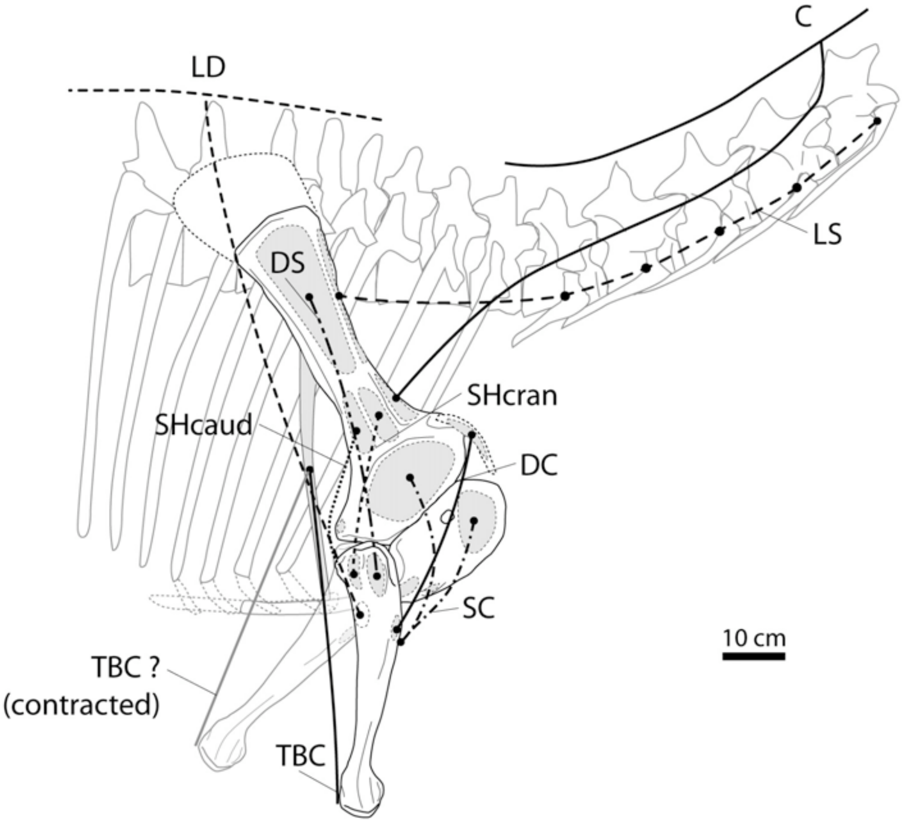

Figure 8-11. Reconstruction of the pectoral skeletomuscular system of *Patagosaurus* in lateral view. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle.

Humerus. The humerus of basal sauropods exhibits many modifications of the plesiomorphic form, most of which can be explained by an alternate, vertical position of the bone. Due to the curvature of the scapulocoracoid and the craniomedial placement of its medial border, the axis of the glenoid joint is not strictly parasagittally, but somewhat caudolaterally oriented. In combination with the form of the humeral head, this leads to an about 30° inward orientation of the developmentally ventral side of the humerus. This configuration has already been recognized in neosauropods (Bonnan, 2003), and applies also to basal forms. The craniocaudal compression, as well as the less sigmoidal shape, may reflect an optimization of the humeral form against axial compression (see Bertram and Biewener, 1988, 1992). The transversely broadened but craniocaudal narrow shaft provides support against lateral bending (which likely occurs during locomotion on uneven ground), but is not optimal if the humerus is retracted far beyond the vertical. The lack of these features in *Kotasaurus* (and probably *Gongxianosaurus*) possibly indicates that the graviportal stance and gait might have been not optimized in these forms, and therefore required additional protection against bending stresses by retaining a circular cross-section of the humeral shaft.

As mentioned above, the configuration of the glenoid prohibits significant protraction of the humerus beyond the vertical in many basal sauropods. As a consequence, the humerus has to be retracted from the vertical for a certain amount in order to generate propulsion; this is reflected in the expansion of the humeral head onto the caudal side of the shaft. In taxa with an especially small coracoidal portion of the glenoid, such as *Cetiosaurus* and *Barapasaurus*, the humerus had slightly more freedom to swing cranially; consequently, the humeral head is reduced caudally but expanded onto the cranial side of the shaft. The reduction of the deltopectoral crest and the proximal shift of its apex relate to reconfigurations of the muscular system and will therefore be discussed below (section ‘Myology’).

The distal end of the humerus exhibits the strongest modifications. Its reduced width relates to a reduction of the intercondylar cavity, bringing both condyles closely together. Based on articulated specimens of neosauropods, it is widely accepted that in sauropods radius and ulna had modified positions relative to other tetrapods, with a caudally placed ulna that forms a secondary articulation between its lateral process and the radial condyle of the humerus. Consequently, the radius is placed cranial to the ulna, avoiding the necessity to cross the ulnar shaft to pronate the hand (Hatcher, 1902, 1903; Gilmore, 1936; Bonnan, 2001, 2003; *contra* Osborn and Granger [1901] and Osborn [1904]; see Wilson and Sereno [1998] for an ‘intermediate’ reconstruction). However, the evolution of the elbow joint in sauropodomorphs is a complex issue that will be discussed in length in the following chapter. Regarding its functionality, the cranially diverging, V-like configuration of the distal articular end of the humerus brings the caudal side of the radial condyle closer to the lateral process of the ulna, and is therefore intimately related to the reorientation of the antebrachium. Hence, the accessory condyles (or rather tubercles) on the cranial edge of the distal end of the humerus might correlate to strong ligaments that hold the radius in place, in its new position craniomedially to the radial condyle. The lack of all of these features in the humerus attributed to *Kotasaurus*, together with the craniocaudal strength and curvature of the shaft, probably indicates that such a pronation system was not yet developed in this form. Nevertheless, the reduction of the outward torsion of the distal end of the humerus in most basal sauropods, including *Kotasaurus*, renders the pronation of the hand easier than in most basal sauropodomorphs (chapter 7).

In comparison, the distal articular surface of mamenchisaurid humeri is highly unusual for sauropods. The wide spacing of the ulnar and radial condyles forces the ulna to develop especially elongate cranial and lateral processes in order to contact both condyles. The function of the unusually formed accessory condyles cannot be assessed from their form alone. Possibly all these modifications, including the outward rotation of the distal end of the humerus relative to the proximal end, may reflect a greater rotational flexibility of the antebrachium against the humerus, which may be related to a specialized type of locomotion (see below).

Antebrachium. An observation that has received some attention in the literature is the lack of an ossified olecranon process in sauropods (Gilmore, 1932; Christiansen, 1997b; Bonnan, 2003; Carrano, 2005). Usually, this is explained by a reduced necessity to extend the forearm in slow, graviportal animals. However, since a distinct olecranon is also missing in 'prosauropods' (animals that probably used their forelimbs partly for grasping and partly for slow, semi-sprawling locomotion), this explanation is not fully convincing. This issue will be discussed in detail in chapter 9, in the context of the evolution of the elbow joint in sauropodomorphs. The aforementioned reconfiguration of radius and ulna in the elbow joint is reflected in the shape of the proximal end of the ulna, which develops an elongate lateral process to articulate with the radial condyle, and a medially rotated cranial process. These modifications bring the whole element from the medial to the caudal side of the forearm. Distally on the ulna, the large, pitted tubercle on the craniomedial side of the distal end may indicate the presence of a strong radioulnar ligament (Upchurch et al., 2004), or a cartilaginous cap that tightly fits into the corresponding surface of the radius. In any case, the radioulnar articulation appears less flexible but more stable than in basal sauropodomorphs. The distal articulation exhibits no obvious specializations, except a slight reduction of the transverse extent of the ulna. Since both the epiphyses and the proximal carpals are unossified, the functionality of the wrist joint cannot be assessed. However, given the semitubular form of the manus (which was already present in *Shunosaurus* and *Omeisaurus*: Upchurch, 1994, 1998; Bonnan, 2003; Upchurch et al., 2004; fig. 8-8C), in combination with the flattened proximal ends of the metacarpals, there was probably not much play to extend and flex the wrist.

The lack of distinct articular surfaces on the ends of sauropod long bones led to a debate about the thickness of the unossified epiphyses in living sauropods (Hotton, 1980; Christiansen, 1997a; Wilson and Sereno, 1998; Holliday et al., 2002; Bonnan, 2003; Schwarz et al., 2007b). Unossified epiphyses are also present in extant archosaurs (Bellairs, 1969; Haines, 1969; Holliday et al., 2002) and other vertebrates (Carter et al., 1998), rendering the indistinct articular surfaces of sauropod long bones not necessarily a special functional adaptation (Carter et al., 1998; Bonnan, 2003). After the discovery of an up to 5 mm thick layer of calcified cartilage on the distal part of the shaft of a sauropod humerus, Schwarz et al. (2007b) suggested that sauropods had epiphyseal cartilage caps that were several centimeters thick, based on isometric scaling of the cartilage caps of extant crocodilians. However, it is unclear if isometric scaling of cartilage caps is plausible over one or two orders of magnitude, since the nutrition of hyaline cartilage depends on diffusion, a process that becomes increasingly inefficient with growing distance (Christiansen, 1997a). Irrespective of this problem, the presence of a thick cartilage cap does not imply that movements of radius and ulna in the elbow joint were restricted to simple hinge-like movements, since the rotational freedom of these bones depends on the *form* of the caps, and on the configuration of the articular ligaments (*contra* Schwarz et al., 2007b). Nevertheless, cartilaginous epiphyses of any thickness protect the growth zone of the bone against axial compression (Parsons, 1905), which appears to have been more advantageous for sauropods than the evolution of fully ossified joint surfaces like in mammals. The reason for this may simply lie in different dynamics of these animals, which may have had no need for securing the joint against unexpected shear stresses that occur during fast moving and running (see Coombs, 1978a).

Manus. Not much can be said about the functional adaptations of the manus in basal sauropods, since this part of the skeleton is in most cases not preserved, and the relevant material could not be examined during this study (see section ‘Data quality’ above). Generally, the distal carpus of sauropods exhibits the strongest ossification proximal to metacarpal I, while the remaining distal carpals are gradually reduced towards the lateral metacarpals. This may be explained by the amphiaxonic structure and only semi-pronated posture of the sauropod manus (see Bonnan, 2003; Carrano, 2005): The highest compressive forces are exerted on the region proximal to digits I and II, because these are oriented in parallel to the vector of progression. For neosauropods, the significance of a tubular arrangement of the metacarpals in combination with digit reduction has been explored in length previously (Bonnan, 2003; Carrano, 2005), clearly indicating that the manus changed its function to a simple weight-bearing structure that played no great role in exerting propulsive force on the ground. Instead, propulsion was primarily generated by the hind limbs (Carrano, 2005). The block-like form of the manual phalanges resembles the ‘prosauropod’ manual type 2 (chapter 7), demonstrating similar functional adaptations. However, the elongate metacarpals (especially metacarpal I) of *Shunosaurus* and *Vulcanodon* resemble the 'prosauropod' manual type 1 (chapter 7). The meaning of these observations for the evolution of the sauropodomorph manus will be discussed in chapter 9. Regarding the function of elongate metacarpals in a manus that has supporting functions only (as indicated by the form of the metacarpus and the reduction of the digits), the most plausible explanation is simply a contribution to the elongation of the entire forelimb (e.g., Upchurch et al., 2007), a development that culminates in the exceptionally long and slender metacarpals of forms like *Brachiosaurus* (see Janensch, 1922, 1961).

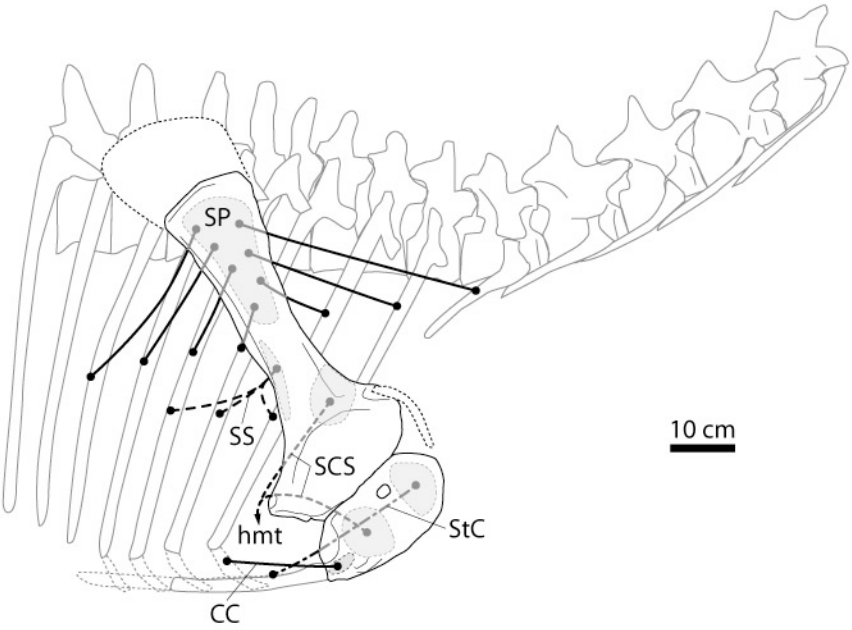

Figure 8-12. Reconstruction of the deep cingulo-axial skeletomuscular system and Mm. subcoracoscapulares in *Patagosaurus* (lateral view). Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle. Shaded areas and lines of action indicate that the muscle lies on the remote side of the bone.

Myology

The reconstructed pectoral skeletomuscular system of *Patagosaurus* is depicted in figs. 8-11 and 8-12. Many features appear plesiomorphic and resemble the pattern found in basal dinosaurs, especially the configuration of the cingulo-axial muscles like the Mm. serrati system (fig. 8-12). The most effective lines of action of M. serratus profundus are found in the region of dorsal ribs 1–4. This may also correlate to the presence of sternal ribs and a sternum in this part of the body, which braced the ribcage ventrally (see Schwarz et al., 2007a). Major modifications may be recognized in connection to the dorsocranial rotation of the scapular head and coracoid: The lines of action of the plesiomorphic protractors of the humerus, M. supracoracoideus and M. deltoideus clavicularis, had a more vertical orientation in basal sauropods, and run closer to the pivot. Thus, these muscles could not serve as effective protractors any longer. This correlates also to the form of the glenoid, which prevents protraction of the humerus much beyond the vertical. Instead, the novel orientation makes these muscles primarily to adductors that stabilize the humerus against dislocations in transverse direction. The size increase of the fossa for M. supracoracoideus pars scapularis on the scapular head may relate to this new function: more muscle mass is concentrated dorsomedially to the humerus, while simultaneously the area for the origin of M. supracoracoideus pars coracoideus is reduced. Due to the alternate position of the humerus, M. pectoralis lost its significance as primary retractor, since its point of insertion (the internal side of the deltopectoral crest) was rather medially than caudally oriented. Therefore, this muscle may have adducted and slightly retracted the humerus, but other muscles must have generated the main retraction movement. Thus, the strong reduction of the deltopectoral crest in sauropods is a direct consequence of the vertical orientation of the humerus, which caused a reduced significance of M. pectoralis and M. deltoideus clavicularis. Possible candidates for alternate retractors are the Mm. scapulohumerales: Due to the reorientation of the humerus, M. scapulohumeralis caudalis inserted somewhat medially to the glenoid, while M. scapulohumeralis cranialis inserted laterally. The wide, flattened, and caudally oriented supraglenoidal facet found in many sauropods might have served as a sliding bearing for M. scapulohumeralis caudalis, or indicates a proximomedially shifted origin of this muscle. However, since the lines of action of Mm. scapulohumerales are relatively short and insert proximally on the humerus, it is not plausible that these muscles have moved the long, heavy limb alone. Aid might have come from M. latissimus dorsi and M. triceps brachii caput coracoscapulare, the latter arising from the sternoscapular ligament (fig. 8-11). Unfortunately, the courses of both muscles and the ligament cannot be inferred reliably, rendering these reconstructions rather speculative. Nevertheless, since the role of the forelimb in generating propulsion was minor in sauropods (Carrano, 2005), there was probably a reduced need for strong humeral retractors.

Other characteristics of the sauropod forelimb probably relate to the vertical orientation of the humerus, too. The wide distance between the lateral tubercle and the humeral head might have been necessary to avoid inference of the inserting M. deltoideus scapularis with M. scapulohumeralis cranialis. On the medial side, the less protruding medial tuberosity possibly indicates a reduced need to rotate the humerus around its long axis, although the origin of M. subscapularis remains in the plesiomorphic position (fig. 8-12; chapters 6–7). The relatively strong development of the medial tuberosity in *Kotasaurus* and *Barapasaurus* resembles the basal sauropodomorph condition, and might indicate that the parasagittal stance and gait was not fully improved in these forms.

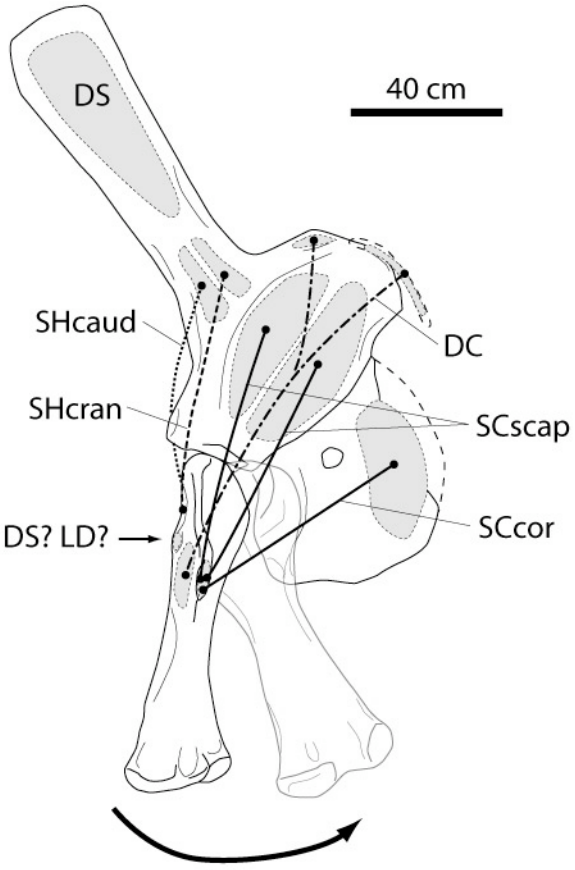

Figure 8-13. Reconstruction of the pectoral skeletomuscular system of *Klamelisaurus* in lateral view. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle.

A large medial tuberosity is also found in mamenchisaurids, but this is probably connected to the unusual shape of the scapular head, glenoid, and elbow joint in this group. The widely open glenoid, its extension onto the external side of the coracoid, and its large size relative to the size of the humeral head indicates an increased rotational freedom of the humerus in the glenoid joint. Moreover, the cranially extended scapular head inflicts a significant craniocaudal component in the course of the lines of action of M. supracoracoideus and M. deltoideus clavicularis. Thus, these sauropods obviously were able to protract the humerus significantly beyond the vertical, avoiding collison with the coracoid by rotating the humerus around its long axis and somewhat onto the lateral side of the coracoid (fig. 8-13). Therefore, the deep furrow craniodorsal to the glenoid in *M. youngi* received the lateral part of the proximal expansion of the humerus during maximum protraction. The enlarged medial tuberosity was necessary to maintain the connection to M. subscapularis during protraction, and to re-rotate the humerus during retraction. The muscle that correlates to the conspicuous tubercle caudolateral to the deltopectoral crest would also have exerted a re-rotational action on the humerus, irrespective if M. deltoideus scapularis or M. latissimus dorsi inserted at this point. Finally, the unusual configuration of the elbow joint, which allowed for greater rotational flexibility but also contained strong ligaments (as indicated by the enlarged accessory tubercles), supports this interpretation. Therefore, mamenchisaurids were adapted for protracting the humerus significantly beyond the vertical, which distinctly increased forelimb step length during locomotion. The most plausible explanation for such an adaptation is a selection towards greater locomotory speed (see Grillner, 1975; Alexander, 1976; Thulborn, 1982). In turn, this might have been advantageous for making more sources of nutrition accessible, due to a reduction of relative locomotory costs.

Compared to the shoulder region, the distal part of the sauropod forelimb exhibits only minor modifications. The smaller biceps tubercle on the coracoid may relate to a reduced significance of M. biceps brachii (see chapter 7). In fact, this may be expected if the forearm and hand are no longer used for grasping. Instead, the role of M. biceps brachii in sauropods would have been restricted to lifting the hand from the ground during the protraction phase of a step cycle. The loss of a distinct caudodistal facet on the distal end of the humerus (which would be distomedially oriented in sauropods) possibly correlates to the reduction or loss of M. flexor digitorum longus (see chapters 5–7). Again, reductions of the digital flexors and extensors may be expected from the structure of the manus. It is highly probable that the reduced area for the origin of M. pronator quadratus on the ulna, and the inferred reduction or loss of M. abductor radialis are related to the reconfiguration of the elbow joint in connection with the cranial placement of the radius. The remaining antebrachial muscles exhibit a largely plesiomorphic pattern, but their attachment sites are slightly twisted distomedially (fig. 8-14). This is a direct consequence of the reorientation of radius and ulna relative to the distal end of the humerus. Given the alternate position of the radius, many of the antebrachial muscles probably served for stabilizing the forearm. However, depending on the form of the humeroradial articulation in the various basal sauropod taxa, a low degree of supination and pronation of the manus would probably have been possible. Finally, the configuration of the M. biceps brachii / M. brachialis system cannot be reliably reconstructed, but any of the configurations proposed for basal sauropodomorphs (chapters 6–7) would have changed its function to a simple flexion of the forearm, since in sauropods the radius is in line with the long axis of the humerus (fig. 8-14).

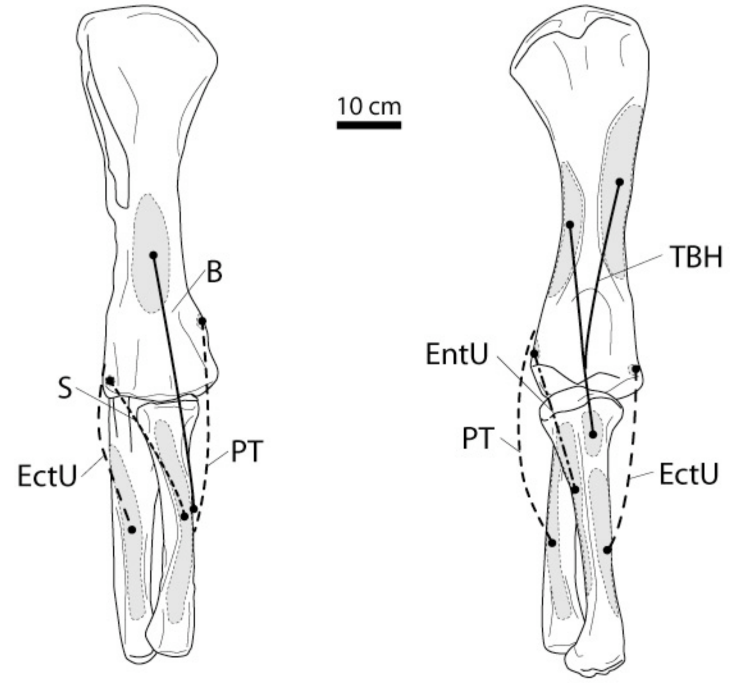

Figure 8-14. Reconstruction of the antebrachial musculature of *Patagosaurus* in craniomedial (left) and caudolateral (right) views. Muscles are depicted by their estimated lines of action, providing a gross idea of the function of each muscle. For explanations see text.

Conclusions

Sauropods had a modified pectoral skeletomuscular system. The ventral part of the shoulder girdle rotated dorsocranially, allowing for a vertical orientation of the humerus. The plesiomorphic protractors and retractors changed their function to adduct and stabilize the humerus, reducing the need for a large deltopectoral crest. The elbow joint is also strongly modified, with a cranially placed radius and a caudally placed ulna that articulates with both the radial and the ulnar condyle. The muscular system of the antebrachium adapted to this reconfiguration, but shows no major changes. The function of the manus changed to pure support, leading to a semitubular arrangement of the metacarpus, and to a reduction of the digits. Some early sauropods lack several of these adaptations (e.g., the humerus attributed to *Kotasaurus*). Mamenchisaurids exhibit a number of specializations in the shoulder girdle and elbow joint that are interpreted as an adaptation for increased speed.

9 Forelimb evolution in sauropodomorphs: Combining functional morphology and phylogeny

Introduction

The evolutionary history of the sauropodomorph forelimb has hitherto not been explored in detail. Ideas about the anatomical evolution of this organ complex, or of the general sauropod *bauplan,* were developed primarily from observations in single genera (Bonaparte, 1971; Bonaparte and Vince, 1979; Cooper, 1984; Yates and Kitching, 2003; Yates and Vasconcelos, 2005; Bonnan and Yates, 2007), from broader comparisons (McIntosh, 1990; Bonnan, 2003), or from the results of parsimony analyses of large data sets of anatomical characters (e.g., Wilson and Sereno, 1998; Wilson, 2002; Upchurch et al., 2007). However, the most parsimonious patterns found in these analyses often indicate a high number of reversals on the line to sauropods, and fail to give functional explanations for the transformations observed. Based on the analyses of the functional morphology of a high number forms on the line to neosauropods, which were presented in the previous chapters, a scenario for the evolution of the pectoral girdle and forelimb of this group will be developed in the chapter at hand. For this purpose, it is essential to select a phylogenetic framework that puts individual observations into an evolutionary context. Such a framework will be introduced and justified in the first section, followed by a summarizing presentation of evolutionary transformations in the sauropodomorph forelimb.

Phylogeny

Since no single analysis currently exists that covers all taxa treated in this work, a ‘consensus’ phylogeny was created by means of combining several published phylogenetic hypotheses (fig. 9-1). However, the word ‘consensus’ is used in a subjective sense here, since no supertree has been calculated. Due to the highly deviant topologies published for basal sauropodomorphs (Gauffre, 1995, 1996; Sereno, 1997, 1999; Benton et al., 2000; Yates, 2001, 2003, 2004, 2007; Hinic, 2002; Martínez, 2002; Yates and Kitching, 2003; Galton and Upchurch, 2004; Pol and Powell, 2007; Upchurch et al., 2007), such an approach would probably result in an unresolved polytomy in this part of the tree. Instead, individual analyses were selected and combined to a phylogenetic hypothesis of the

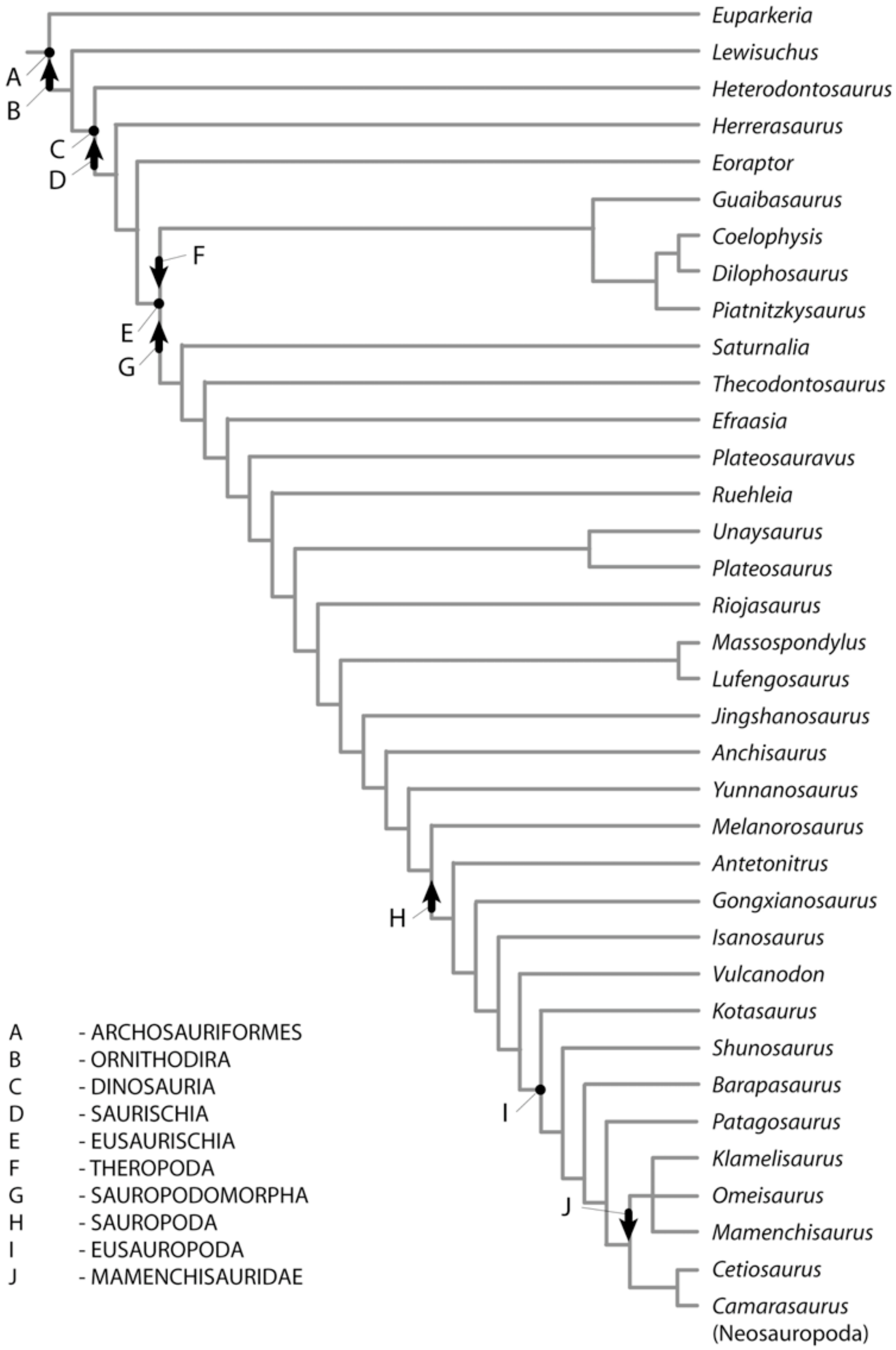

Figure 9-1. Cladogram of saurischian and outgroup taxa treated in this thesis. Combined after Wilson (2002), Rauhut (2003a), Benton (2004), Upchurch et al. (2004, 2007), Langer and Benton (2006), and Yates (2007). For explanations see text.

taxa covered in this thesis. Recent analyses with a high number of characters and taxa have been preferred, since these are assumed to be more adequate in terms of reflecting the osteological differences among the individual taxa, and in avoiding coding biases towards certain body regions. However, the optimal number of characters for a given set of OTUs is methodologically debated (see Rieppel, 1999). Therefore, this approach can only be regarded as preliminary, until a highly resolved consensus on basal dinosaur and sauropodomorph relationships is established. The reasons for the selections made will briefly be discussed in the following.

Euparkeria is recognized as an outgroup to crown-group Archosauria in all published phylogenetic analyses of archosauromorphs (see Gower and Wilkinson [1996] and Benton [2004] for reviews), with the exception of Gauthier (1986), who found *Euparkeria* to be more closely related to Ornithodira than to Crocodylomorpha. Since no other archosauriforms, crurotarsans or basal ornithodirans are included in this analysis, the placement of *Euparkeria* as the sister group to Dinosauriformes is justified here.

Lewisuchus has not been included in a numerical phylogenetic analysis yet. Based on Arcucci's (1997) assignment of this form to Dinosauromorpha, as a possible subjective senior synonym of *Pseudolagosuchus*, it seems established that *Lewisuchus* is more closely related to Dinosauria than *Euparkeria*, but stands outside the ornithischian-saurischian dichotomy, as proposed for other Ladinian dinosauromorphs (Gauthier, 1986; Benton and Clark, 1988; Novas, 1992, 1996; Juul, 1994; Bennett, 1996; Fraser et al., 2002; Benton, 1999, 2004).

The tree topology of basal dinosaurs largely follows Langer (2004) and Langer and Benton (2006), who analyze a matrix of 10 OTUs and 98 coded characters. Early examinations of basal dinosaur relationships found Herrerasauridae to fall outside Ornithischia+Saurischia (Gauthier, 1986; Brinkman and Sues, 1987; Benton, 1990; Novas, 1992), but in more recent analyses, *Herrerasaurus* and *Eoraptor* cluster within Saurischia (but see Fraser et al., 2002). However, opinions diverge if these taxa are more closely related to theropods than to sauropodomorphs (Novas, 1996, 1997; Sereno, 1997, 1999; Rauhut, 2003a; Benton, 2004), or stand outside Eusaurischia (Holtz, 1995; Langer, 2004; Langer and Benton, 2006). Langer (2004), Langer and Benton (2006), and Upchurch et al. (2007) provide analyses that include *Guaibasaurus* as an OTU, and consistently found this taxon to plot as a stem-theropod.

The topology within Eutheropoda is based on Rauhut (2003a), but may be regarded as consensus on theropod interrelationships (see Tykoski and Rowe, 2004, and Holtz et al., 2004, for reviews). Moreover, it is consensus that *Saturnalia* is the basal-most sauropodomorph known, since this taxon consistently plots at this position in almost all published analyses (Langer et al., 1999; Yates, 2001, 2003a; Langer, 2004; Langer and Benton, 2006; Upchurch et al., 2007). Only Galton and Upchurch (2004) found *Saturnalia* to be more derived than *Thecodontosaurus*.

Admittedly, the choice of the analysis of Yates (2007) as a template for the relationships within basal sauropodomorphs can only be justified by the high number of coded characters (384 characters for 46 OTUs). There is no consensus for basal sauropodomorph ingroup relationships among recent analyses. For instance, Galton and Upchurch (2004) found monophyletic Prosauropoda (137 characters, 24 OTUs), while Upchurch et al. (2007) discovered a monophyletic cluster of 'core'-prosauropods. In this topology, *Mussaurus* and *Efraasia* are stem-sauropodomorphs, and *Jingshanosaurus*, melanorosaurids and *Antetonitrus* are stem-sauropods (292 characters, 34 OTUs). Moreover, not a single sister-group relationship found in the analysis of Yates (2007) is reproduced in the analyses of Galton and Upchurch (2004) or Upchurch et al. (2007). Therefore, the topology of this part of the tree can only be regarded as a preliminary result, and is likely to change in future analyses. Nevertheless, one crucial consensus between Yates (2007) and Upchurch et al. (2007) is the placement of *Melanorosaurus* and *Antetonitrus* at the root of the Sauropoda. *Anchisaurus* has also been regarded as a basal sauropod (Yates and Kitching, 2003; Yates, 2004), but the support for such a phylogenetic position is weak (Fedak and Galton, 2007).

The relationships within basal sauropods are combined after Wilson (2002) and Upchurch et al. (2004). These works differ in two aspects from Upchurch et al. (2007): Wilson (2002) and Upchurch et al. (2004) found *Barapasaurus* to be more closely related to Neosauropoda than *Shunosaurus*, but the reverse is the case in Upchurch et al. (2007). Moreover, *Kotasaurus* is regarded as more closely related to eusauropods than *Vulcanodon* in the former works, but both taxa again change places in Upchurch et al. (2007). It is probable that different focuses in the analyzed data matrices produce this effect, and a combined analysis of basal sauropodomorphs and sauropods might help to find a consensus here. For the moment, the results of the works that concentrate on sauropod interrelationships are preferred, since the level of consensus among the various published analyses is considerably higher than in basal sauropodomorphs. The sister group relationship between *Klamelisaurus* and mamenchisaurids is based on own observations and discussions (Rauhut, pers. comm. 2006), but has not been confirmed yet in a numerical cladistic analysis. Finally, the sister-group relationship between *Cetiosaurus* and Neosauropoda is supported by Upchurch and Martin (2002) and Yates (2007).

Evolutionary transformations

Combining the results of chapters 4 to 8 with the phylogenetic framework introduced in fig. 9-1, the evolutionary history of important character complexes of the sauropodomorph forelimb will be described in the following.

Pectoral girdle

Structure. The pectoral girdle experienced some significant modifications on the line to neosauropods, but preserved a relatively conservative structure: The scapular blade remains caudodorsally oriented (see below), and the coracoid retains a plesiomorphic, suboval shape. Basal archosaurs like *Euparkeria* have a robust pectoral girdle that is about as wide as high, and retain large coracoids and a primarily caudolaterally directed glenoid. Long, robust clavicles that connect to a bony interclavicle near the median line brace the girdle cranially (fig. 9-2). In dinosauriforms, the robustness of the girdle is reduced, and it becomes transversely narrow. This indicates a dorsoventrally high but transversely slender torso, which is probably related to increased cursoriality (however, this does not imply obligate bipedalism; see chapter 4). *Lewisuchus* represents an intermediate stage in this respect, but *Eoraptor* and most basal sauropodomorphs have a girdle that is about twice as high as it is wide in cranial view. Only *Saturnalia* exhibits a stage that is intermediate between *Lewisuchus* and *Eoraptor*, with a dorsally narrow but ventrally wide pectoral girdle. In parallel to the advent of a transversely slender body profile, the interclavicle was lost. Possibly, this stands in connection to a less sprawling posture, which reduced the lateral pressure on the girdle during locomotion. A direct midline articulation of both clavicles, dorsal to the ventral surface of the body, might also have been a factor that facilitated the reduction of the interclavicle. This novel kind of articulation was probably brought forth by the transverse narrowing of the torso.

Clavicles. Clavicles are rarely preserved in dinosaurs, but must have been present in all Saurischia (and therefore also in their dinosauriform ancestors), as demonstrated by their repeated occurrence in non-maniraptoran theropods

(Camp, 1936; Chure and Madsen, 1996; Makovicky and Currie, 1998; Tykoski et al., 2002; Carrano et al., 2005; Larson and Rigby, 2005; Rinehart et al., 2007), basal sauropodomorphs (von Huene, 1926; Yates and Vasconcelos, 2005), and sauropods (Hatcher, 1901, 1903; Dong et al., 1983; Zhang et al., 1984; He et al., 1988; Zhang, 1988; Sereno et al., 1999). Moreover, most sauropodomorphs have a distinct facet on the acromion that indicates the clavicular articulation (chapters 6–8). Possibly, there is a taphonomic bias against the preservation of clavicles, due to their minute structure, their weak connection to the pectoral girdle, and their position within a probably carnivore-attracting muscle mass between neck and deltoid muscles. Hence, it is inferred here that clavicles were always present on the evolutionary line to sauropods, bracing the pectoral girdle cranially, and serving as the site of origin of M. deltoideus clavicularis.

Scapulocoracoid orientation. As mentioned in chapter 2, the orientation of the scapulocoracoid relative to the axis of the vertebral column has been a matter of debate. Based on an articulated specimen of *Camarasaurus* described by Gilmore (1925), it was assumed for a long time that the scapular blade was rather horizontally than vertically oriented, leading to a terminology that described the acromion as projecting dorsally above the scapular blade (e.g., Upchurch, 1998; Upchurch et al., 2004). Parrish and Stevens (2002) suggested that facets on the lateral sides of the dorsal ribs of a specimen of *Apatosaurus* indicate the natural position of the scapular blade, in this case, a near-horizontal orientation. Other workers reconstructed the scapula inclined with 30° to the horizontal (e.g., Wilhite, 2005), or with 45° (e.g., Stevens and Parrish, 2005b). However, in order to evaluate these different models, any reconstruction should be tested in both a phylogenetical and a functional context. Phylogenetically, the starting point for the evolution of sauropods is a form like *Euparkeria*, being characterized by broad, ventrally facing coracoids that are oriented in the same plane as the caudally adjacent (but unossified) sternum. Based on extant Reptilia (including birds), it can be phylogenetically inferred that the sternum articulated via sternocostae with the cranial dorsal ribs, which exhibit thickened and rugose termini on their ventral ends for this purpose (e.g., Cong et al., 1998; Baumel and Witmer, 1993). Hence, there are several constraints for the reconstruction of the scapulocoracoid position in dinosaurs that usually have been disregarded (Schwarz et al., 2007a):

- The coracoid has to articulate with the sternum
- In all extant amniotes, the sternum is oriented in parallel to the distal ends of the dorsal ribs, which in most cases comes up to an orientation in parallel to the dorsal vertebral column

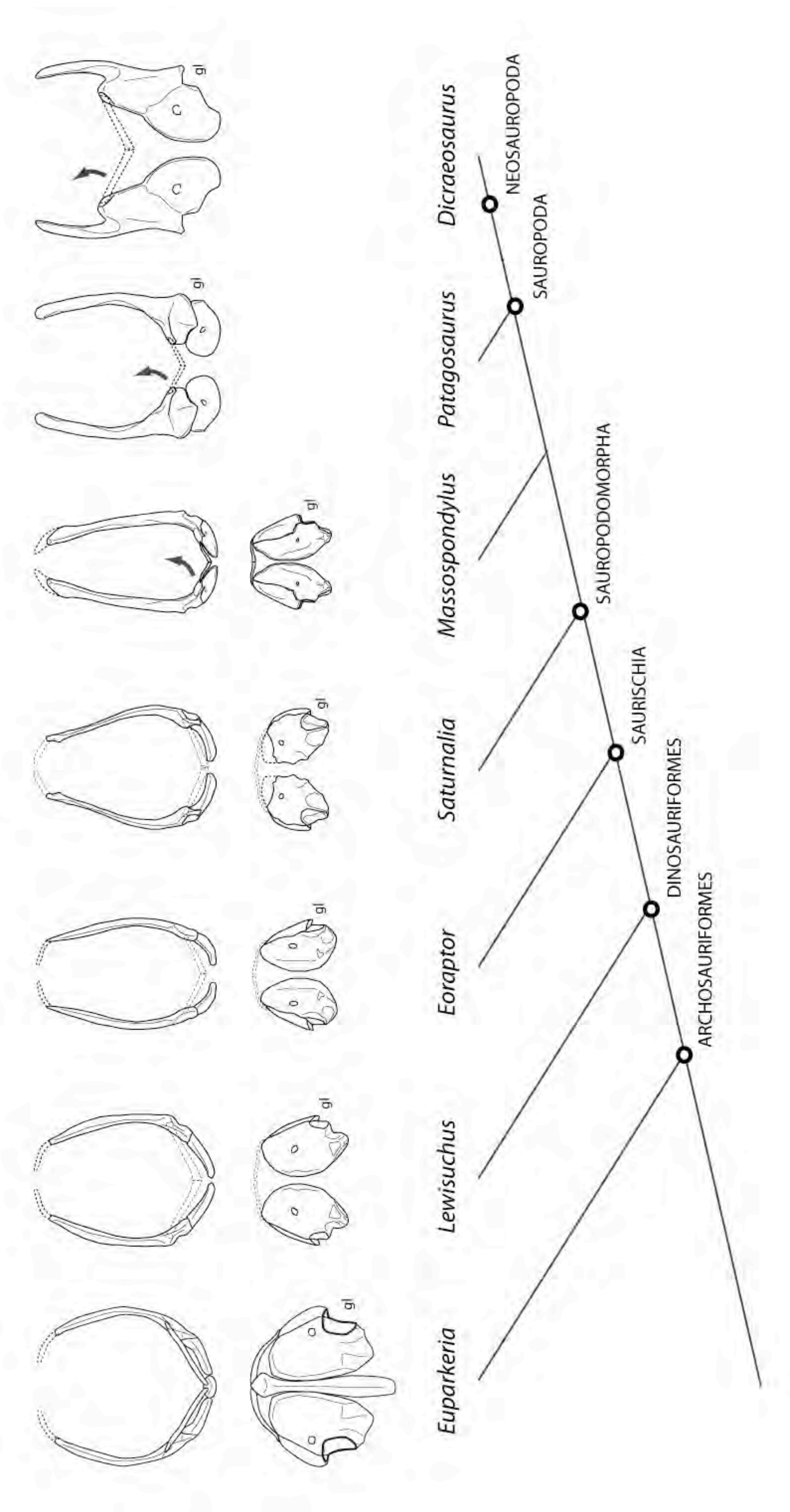

Figure 9-2. Cladogram of transformations of the pectoral girdle on the line to neosauropods. Above, cranial view; below, ventral view. Note the cranial rotation of the ventral pectoral girdle in sauropods.

- The sternum has to be in such a position relative to the coracoid that its articulation with the ribcage via the sternal ribs is maintained

A horizontal position of the scapula, like in birds and higher maniraptorans, has therefore only been possible by a dorsoventral elongation of the coracoid and a backward inclination of the scapular blade relative to the central axis of the coracoid (see Ostrom, 1974, 1976; Carpenter, 2002; Gatesy and Baier, 2005; Senter, 2006b). On the evolutionary line to the sauropods, none of these modifications are visible. In dinosauriforms, the coracoid is reduced in size relative to the scapula, and curves somewhat dorsocranially, slightly more so than in *Euparkeria*. In sauropodomorphs more derived than *Saturnalia*, this effect is enhanced, and the plesiomorphic ventromedial edge of the coracoid becomes more ventrocranially directed. This is made possible by a smaller angle between the long axis of the scapular blade and the long axis of the scapular head. In *Lewisuchus,* both axes form an angle of about 100°. The axes stand perpendicular to each other in most basal sauropodomorphs, but are increasingly sharply angled in basal sauropods, and reach 45° or less in neosauropods (fig. 9-3). The beginning of this cranial rotation of the ventral part of the pectoral girdle is first visible in *Isanosaurus*, and Middle Jurassic eusauropods exhibit an intermediate stage between basal sauropodomorphs and neosauropods (fig. 9-3). The only alternative to this interpretation would be a cranial rotation of the scapular blade; however, this can be rejected because it would imply a dorsal rotation of the glenoid, and create nonfunctional lines of action for Mm. serrati and M. deltoideus scapularis (fig. 9-4). Therefore, the inclination of the scapular blade remains plesiomorphic during the entire evolutionary history of the sauropodomorphs, about 60° relative to the horizontal. A lesser angle, i.e. a backward rotation of the entire scapulocoracoid in addition to the cranial rotation of the ventral part of the girdle, would create disarticulation either in the sternocoracoidal joint, or between the sternum and the sternocostae. Moreover, the clavicles would come to a horizontal orientation, which would be highly unusual among amniotes, and would prevent effective attachment of the neck musculature (fig. 9-4). Based primarily on comparisons with extant diapsids, Schwarz et al. (2007a) independently came to similar results for three neosauropod genera.

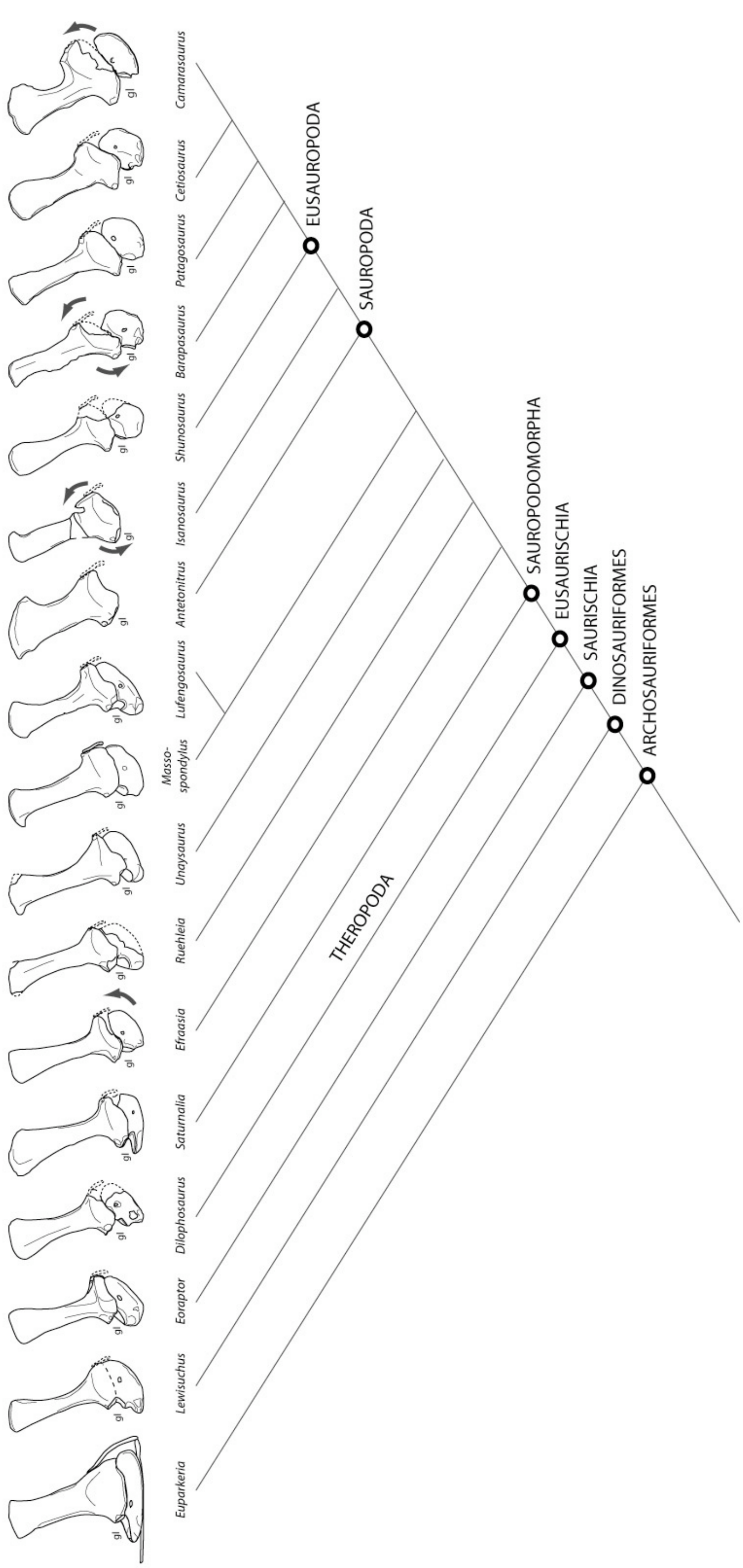

Figure 9-3. Cladogram of the transformations of the scapulocoracoid on the line to neosauropods. The cranial rotation of the ventral part of the pectoral girdle is indicated by arrows. For explanations see text.

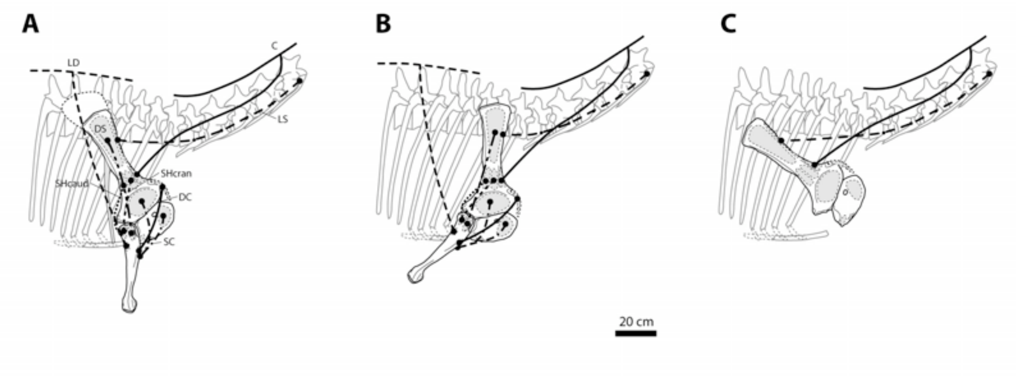

Figure 9-4. Comparison of different interpretations of the scapulocoracoid orientation in sauropods. **A**, position based on tracking of character evolution as developed throughout this thesis. A 60° inclination relative to the horizontal was also found by Schwarz et al. (2007a), based primarily on comparisons with recent amniotes. **B**, alternate interpretation of the observed transformations. A cranial rotation of the scapula blade would bring the glenoid into an unlikely position, rendering the humerus caudally inclined. **C**, classical reconstruction of Gilmore (1925), causing disarticulation between coracoid and sternum and bringing the clavicles into an unlikely position.

Sternal plates. In parallel with the beginning reorientation of the ventral part of the pectoral girdle, sauropodomorphs acquire ossifications within the sternum. The craniolateral corners of these sternal plates articulate with the caudomedial corners of the coracoids, as indicated by the thickened, rugose tubercles on both elements. It is proposed here that the ossification of sternal plates and the dorsocranial angulation of the coracoid relative to the plane of the sternum are causally related. The ossification stabilizes the sternocoracoidal joint by forming a prop against shear stresses that result from the oblique orientation of the coracoid during locomotion. Moreover, it provides a stable base for the origin of M. sternocoracoideus (a plesiomorphic muscle that was lost in crocodiles but retained in dinosaurs, see chapter 3), which helps to keep the coracoid in place (fig. 9-5). With increasing angle between coracoid and sternum, the sternal plates also seem to increase in size, but this pattern has not been tested for neosauropods.

Scapula. Other characters of the scapulocoracoid show no clear evolutionary trend. Under the tree topology applied here, the form and extent of the distal expansion of the scapular blade varies considerably, as well as the position and size of the caudal flange. *Yunnanosaurus, Melanorosaurus* and *Antetonitrus,* which stand close to the origin of sauropods, exhibit an increased craniocaudal width of the scapular blade relative to the width of the scapular head. However, basal sauropods lack this character, and have slender scapulae that resemble those of other basal sauropodomorphs (fig. 9-3). Since it cannot be reconstructed reliably if one or more of these characters were crucial for a modified function of the forelimb (chapters 7, 8), these variations may contain no phylogenetic signal at all, but might be due to intergeneric morphological variation that provides taxonomic information only. However, it is also possible that the current phylogenetic hypotheses of basal sauropodomorphs are still too far from the actual historical pattern, and therefore fail to bring these minor modifications into the right order.

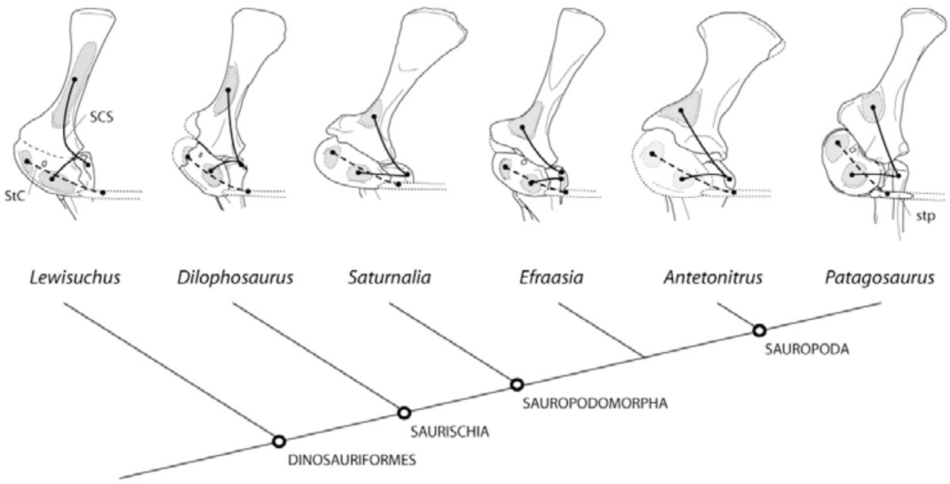

Figure 9-5. Cladogram illustrating the changes in the medial shoulder girdle musculature. For explanations see text.

Coracoid. In the course of sauropod evolution, the coracoid shows comparatively little changes. Due to the cranial rotation of the ventral part of the pectoral girdle, the craniocaudal extent of the coracoid is successively reduced, as well as its size relative to the scapular head (fig. 9-3). Variation can be observed in two other characters: First, the size of the biceps tubercle considerably increases in taxa that exhibit specializations towards grasping or raking (e.g., theropods, *Unaysaurus, Plateosaurus*), but also quadrupeds with semi-erect forelimbs like *Lufengosaurus* and *Yunnanosaurus*. In the graviportal sauropods, the biceps tubercle is reduced. However, the data about this character is sparse for the transitional forms *Melanorosaurus, Antetonitrus, Isanosaurus,* and *Gongxianosaurus*. Second, the subglenoid fossa (the attachment of M. costocoracoideus) is deep with a strong lateral ridge in *Eoraptor, Herrerasaurus, Saturnalia* (no clear lateral ridge)*, Riojasaurus, Coloradisaurus, Plateosaurus, Lufengosaurus, Massospondylus,* and *Barapasaurus*, but reduced to a saddle-shaped facet in other sauropodomorphs. The form of this fossa therefore contains no obvious phylogenetic signal, but considering this pattern of taxonomic distribution, it is also hard to find functional explanations.

Glenoid joint. The cranial rotation of the ventral part of the pectoral girdle affects the orientation of the glenoid, which is reoriented from a plesiomorphic ventrolateral (*Euparkeria*) via a caudoventrolateral (basal dinosaurs) to a ventral orientation in sauropods. In basal archosaurs, the coracoidal part of the glenoid is large relative to the scapular part. It supports the semi-erect humerus medially, and diverts the main component of the ground reaction forces, which are transferred via the humerus. In this configuration, the scapular part of the glenoid primarily holds the humerus in place but receives comparatively little pressure. In basal dinosaurs and sauropodomorphs, both parts of the glenoid become equally sized, indicating that the humerus was hold in a more erect position (in basal sauropodomorphs like *Anchisaurus* and *Massospondylus*, around 20-30° relative to the vertical), but a parasagittal posture was not possible prior to the cranial rotation of the coracoid. The coracoid rotation gave way for an erect humerus, enabling an almost complete transfer of the pressure exerted by ground reaction forces onto the scapular part of the glenoid, which in turn considerably enlarges in sauropods (figs. 9-3, 9-6). As a consequence, the coracoidal part of the glenoid is reduced in size relative to the scapular part; it mainly provides support to hold the humerus in place during retraction, and therefore forms a prop against the parasagittal component of the ground reaction forces that occur during locomotion. However, this system restricts the possibility to protract the humerus, leading to a short step length and therefore limited speed. Mamenchisaurids circumvented this disadvantage by a specialized glenoid joint and shoulder muscle system that allowed the humerus to rotate laterally around the coracoid (chapter 8). Nevertheless, the limited ability of humerus protraction is retained in neosauropods.

Humerus

General aspects. During sauropodomorph evolution, the cranial rotation of the ventral part of the shoulder girdle reoriented the humerus and the cranial shoulder muscles that act on this bone, leading to a number of modifications. The general form of the humerus, with a craniocaudally wide humeral head, a large deltopectoral crest, a slender shaft and a dilated distal end that is rotated cranially with respect to the proximal expansion, is already found in *Euparkeria* and therefore plesiomorphic for archosaurs. The slender humerus and short deltopectoral crest of *Lewisuchus* may either be an autapomorphic specialization that does not reflect the main trend of dinosauriform forelimb evolution, or *Eoraptor, Guaibasaurus* and sauropodomorphs reversed to the plesiomorphic condition.

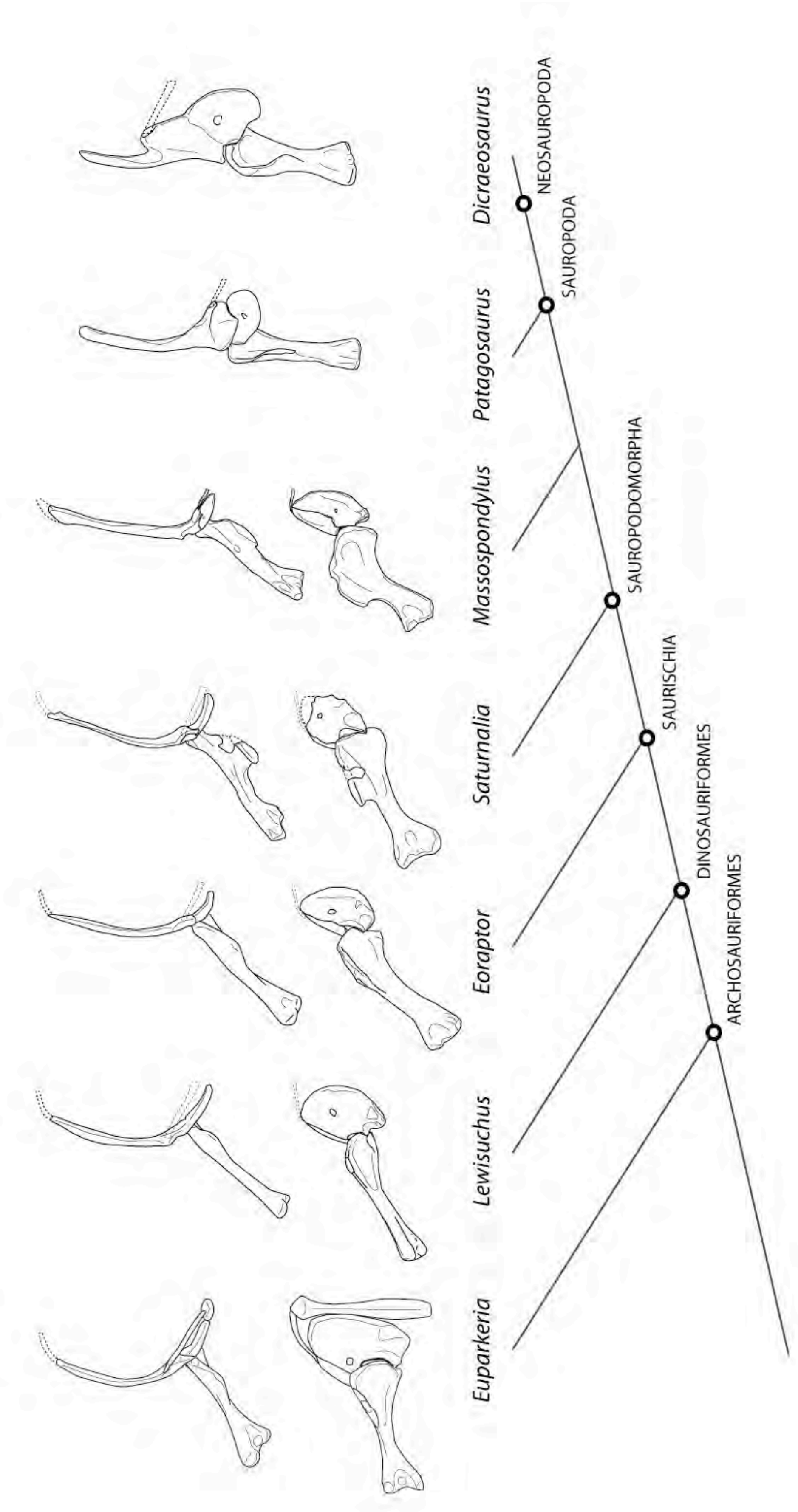

Figure 9-6. Cladogram of the changes in humeral posture due to the re-configuration of the pectoral girdle on the line to neosauropods. Above, cranial view; below, ventral view.

Given the poor record of basal dinosauriform forelimbs, the first explanation currently appears to be more parsimonious.

In Jurassic ‘prosauropods’, *Antetonitrus* and basal sauropods, the humeral head becomes convexly vaulted over the level of the medial tuberosity and deltopectoral crest, probably correlating with an increased flexibility of the humerus in the glenoid joint. Moreover, the head develops a pronounced extension onto the developmentally dorsal side of the shaft, which may be related to a more erect position of the humerus in the glenoid joint. Both features are reduced again in many neosauropods and indicate a change towards a simple hinge-like, parasagittal movement.

Plesiomorphically in archosaurs, the humerus is abducted and elevated by Mm. scapulohumerales and M. latissimus dorsi, possibly aided by a M. teres major that arose from the scapular blade (chapter 3). The antagonist, M. coracobrachialis, adducts the humerus and therefore elevates the torso relative to the ground when the animal stands or walks quadrupedally. A distinct scar on the dorsal side of the humerus marks the insertion of M. latissimus dorsi, while M. coracobrachialis inserts in a large, deep fossa proximally on the ventral side of the humerus. This system is retained in sauropodomorphs, but the craniolateral shift of the insertion of M. latissimus dorsi adds a new, rotational component to the action of this muscle. The evolution of this system cannot be clearly traced in *Yunnanosaurus, Melanorosaurus, Antetonitrus*, and sauropods, due to a reduction of the osteological correlates, but it appears that sauropods evolved a fleshy insertion of this muscle and reversed its site of insertion to the plesiomorphic position, directly distal to the humeral head. Combined with the erect position of the humerus and the caudal rotation of its developmentally dorsal side, M. latissimus dorsi will then have acted as a humeral retractor (chapter 8).

The presence of a distinct intercondylar pit on the developmentally ventral side of the humerus is a plesiomorphic trait of archosaurs that probably correlates to a flexed elbow during locomotion (chapters 6, 7). Such a depression is retained in *Eoraptor, Saturnalia* and most basal sauropodomorphs, but reduced in the obligate bipedal form *Herrerasaurus*, theropods, and the graviportal eusauropods (fig. 9-7). Together with other plesiomorphic properties (see chapter 8), the humerus attributed to *Kotasaurus* shares this character, possibly indicating that an erect limb was not yet fully developed in this form (i.e., the humerus was possibly abducted with 5 to 10°). Moreover, most basal sauropodomorphs and early theropods develop a distinct facet adjacent to the ulnar condyle, which is inferred to have served for the origin of M. flexor digitorum longus (chapters 5–7). Since such a facet is not clearly developed in *Eoraptor* and *Herrerasaurus*, its presence seems to constitute a grasping-related eusaurischian synapomorphy that was reduced in sauropods in parallel with the reconfiguration of the manus (fig. 9-7; see below).

Other changes in the orientation and form of the distal expansion of the humerus will be discussed in the section 'Elbow joint' below.

Deltopectoral crest. Due to the semi-erect position of the humerus and the ventrolateral orientation of the glenoid, the deltopecotral crest is ventrally to cranioventrally oriented in basal archosaurs (*Euparkeria*) and basal dinosaurs, including *Eoraptor* and *Saturnalia*. Sauropodomorphs considerably increase the size of the crest, indicating the importance of the muscular system that inserts on this structure. This system includes M. pectoralis, M. deltoideus clavicularis, and M. supracoracoideus, and is the plesiomorphic protraction-retraction system in amniotes (Hildebrand and Goslow, 2001). The enlargement of this system in sauropodomorphs may in part correlate to an increase in body size without changing the semi-erect forelimb position, forcing the musculature to scale with positive allometry (Biewener, 1989a, 1990, 1991). However, the enlarged crest is already present in *Saturnalia*, a form that is not considerably larger than *Eoraptor*. Therefore, the evolution of an additional forelimb function, i.e., powerful grasping and bending of branches and other parts of the vegetation, might be another driving force behind this modification. With the reorientation of the ventral part of the shoulder girdle and the glenoid, the lines of action of the M. pectoralis – M. deltoideus clavicularis – M. supracoracoideus system are also reconfigured (fig. 9-8). These muscles largely kept their plesiomorphic orientation in basal sauropodomorphs, but the rotation of the ventral pectoral girdle and erect position of the humerus in sauropods reduces the effectiveness of M. deltoideus scapularis as a protractor, while M. supracoracoideus loses the function as adductor and becomes the new primary protractor. This is also indicated by the relative enlargement of the supracoracoideus fossa on the scapular head, a trend continued in neosauropods. Simultaneously, adduction is taken over by M. pectoralis, and also by M. subscapularis. The latter muscle has cranially shifted in sauropodomorphs plesiomorphically, aiding in humeral rotation (chapters 6, 7), but re-acquires a more vertical orientation in sauropods (fig. 9-5).

A change to a dominance of proximal humeral retractors accompanied by a reduction of the forearm extensors, as predicted by Christiansen (1997a) and Carrano (2005) for quadrupedal, graviportal animals, cannot be unambiguously recognized on the evolutionary line to sauropods. Despite a reduction of the olecranon process, sauropods preserve distinct striations on the caudal face of the caudal ulnar process (insertion of M. triceps brachii), and the facets on the caudal humeral shaft provide much room for the origin of Mm. triceps brachii capiti humerales. As discussed in chapter 3, the size of an osteological correlate of a muscle is not necessarily correlated with the volume of this muscle in the living animal. Given that the humerus in sauropods could not be protracted far beyond the vertical, forearm extension and flexion may have been more important for locomotion than in graviportal mammals, a question worth to explore in future biomechanical simulations.

Elbow joint

Bonnan (2001, 2003) noted that the manus of saurischian dinosaurs plesiomorphically could not be fully pronated, due to the elongate cranial ulnar process that prevents the radius to cross in front of the ulna. He found that manus pronation in sauropods was only possible by a cranial rotation of the radius and a simultaneous elongation of the ulnar lateral process, which developed a secondary articulation with the caudal part of the radial tubercle. Yates and Kitching (2003) and Bonnan and Yates (2007) described an enlarged lateral process on the ulnae of *Antetonitrus* and *Melanorosaurus*, respectively, and interpreted this as the beginning of the development that enabled the radius to rotate cranially, and that finally led to the L-shaped proximal end of the sauropod ulna.

With a phylogenetic perspective on the sauropodomorph elbow joint evolution, these results have to be modified to a certain degree. The argumentation of the works cited above is based on the assumption that the radius articulates in the radial fossa of the ulna, and that hence the form of the ulnar radial fossa provides information about possible movements of the radius. However, in extant diapsids and also in archosaurs plesiomorphically, the radius does not articulate with the ulna cranial to the lateral process, but both bones are widely separated in the elbow joint (*Euparkeria* in fig. 9-8C; Haines, 1946; Ewer, 1965; Landsmeer, 1983, 1984). Thus, the configuration and form of the distal condyles of the humerus provides more accurate information about possible movements and restrictions of radius and ulna. However, since the humeral epiphyses are unossified, such an assessment can only be gross, and limits in the grade of rotation, flexion, and extension are hard to determine.

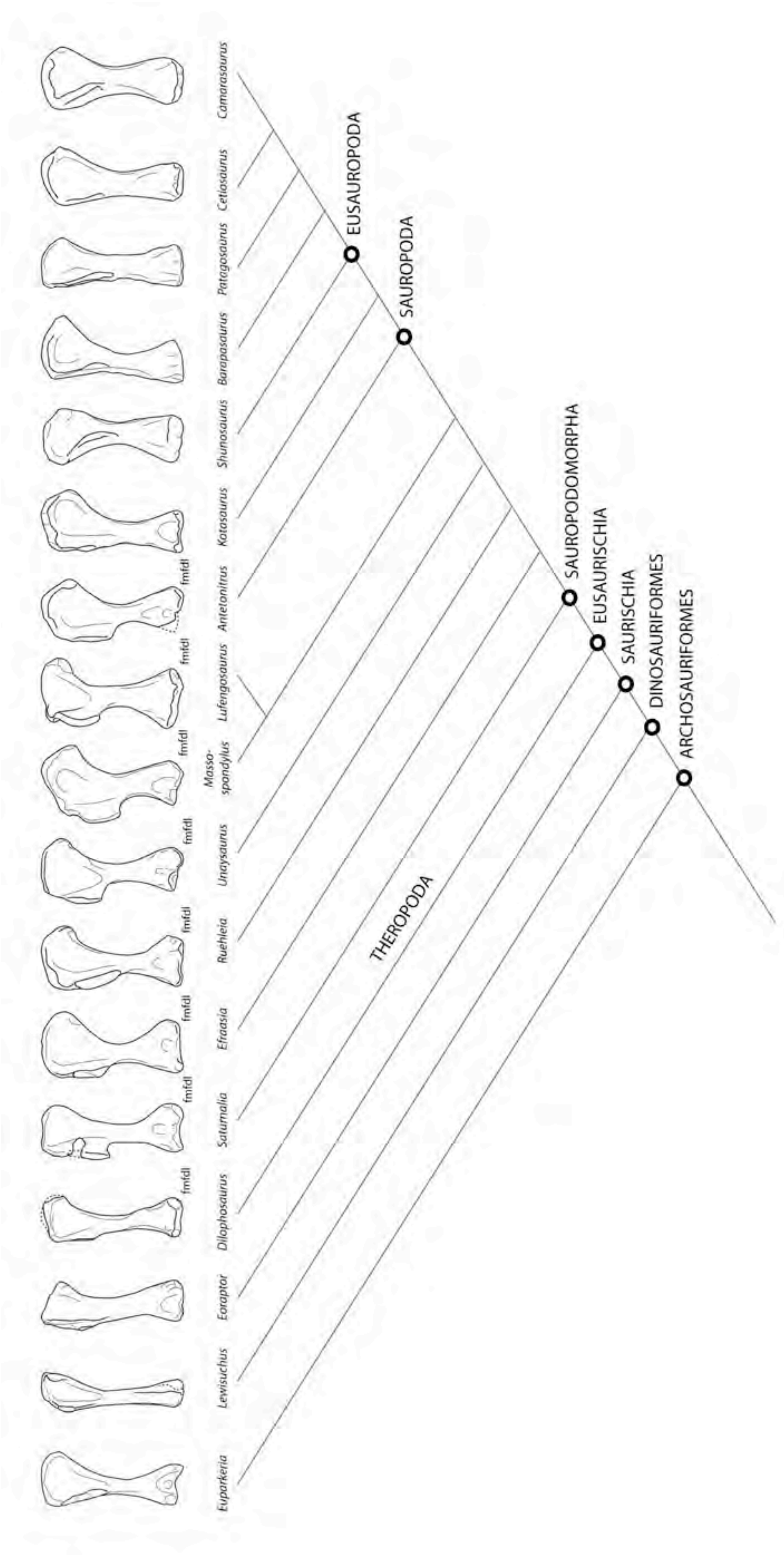

Figure 9-7. Cladogram of the transformations in humeral shape on the line to neosauropods. The humeri are shown in ventral view.

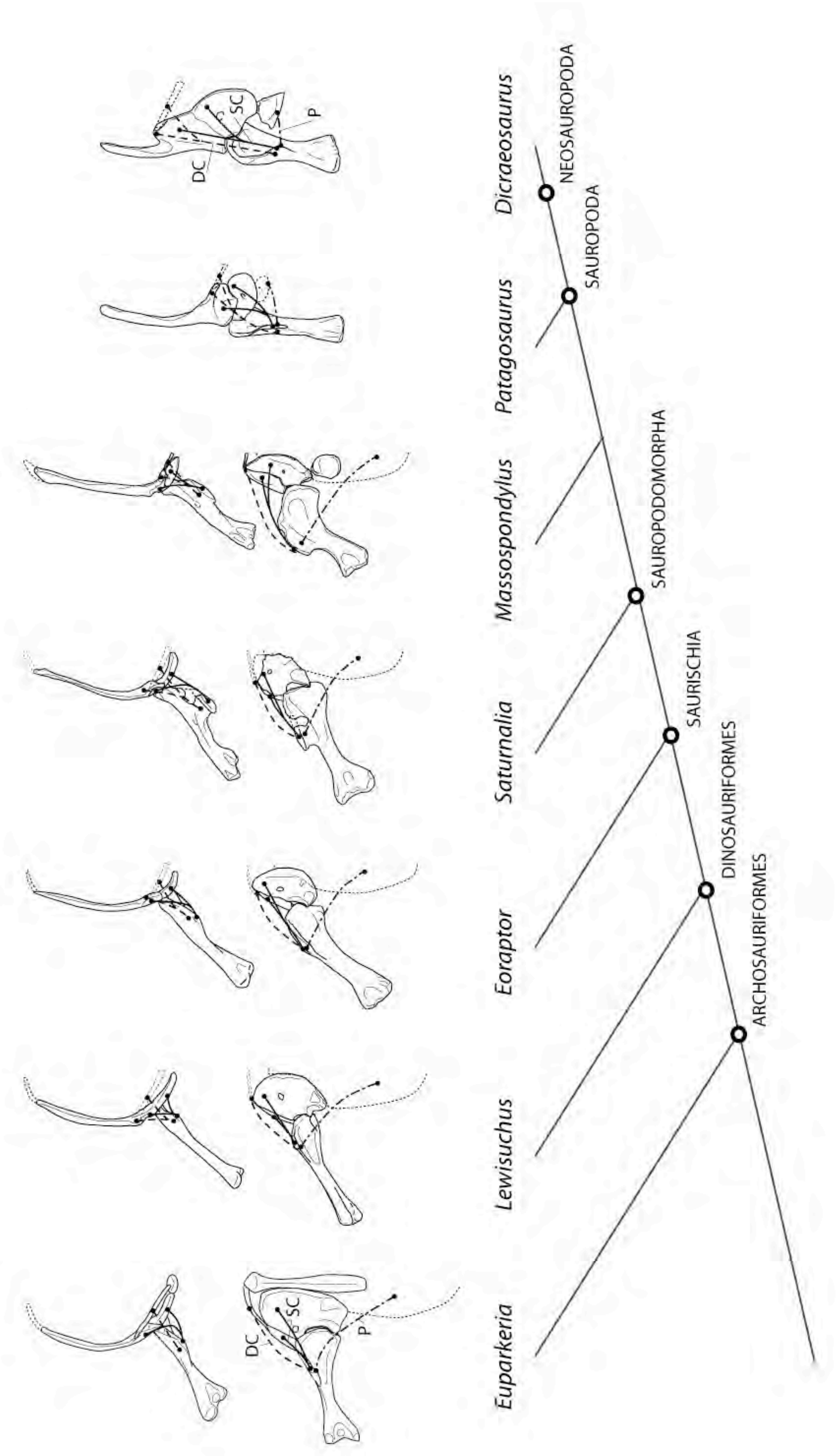

Figure 9-8. Cladogram of the transformations of the deltoid, pectoralis, and supracoracoideus musculature on the line to neosauropods. Above, cranial view; below, ventral view.

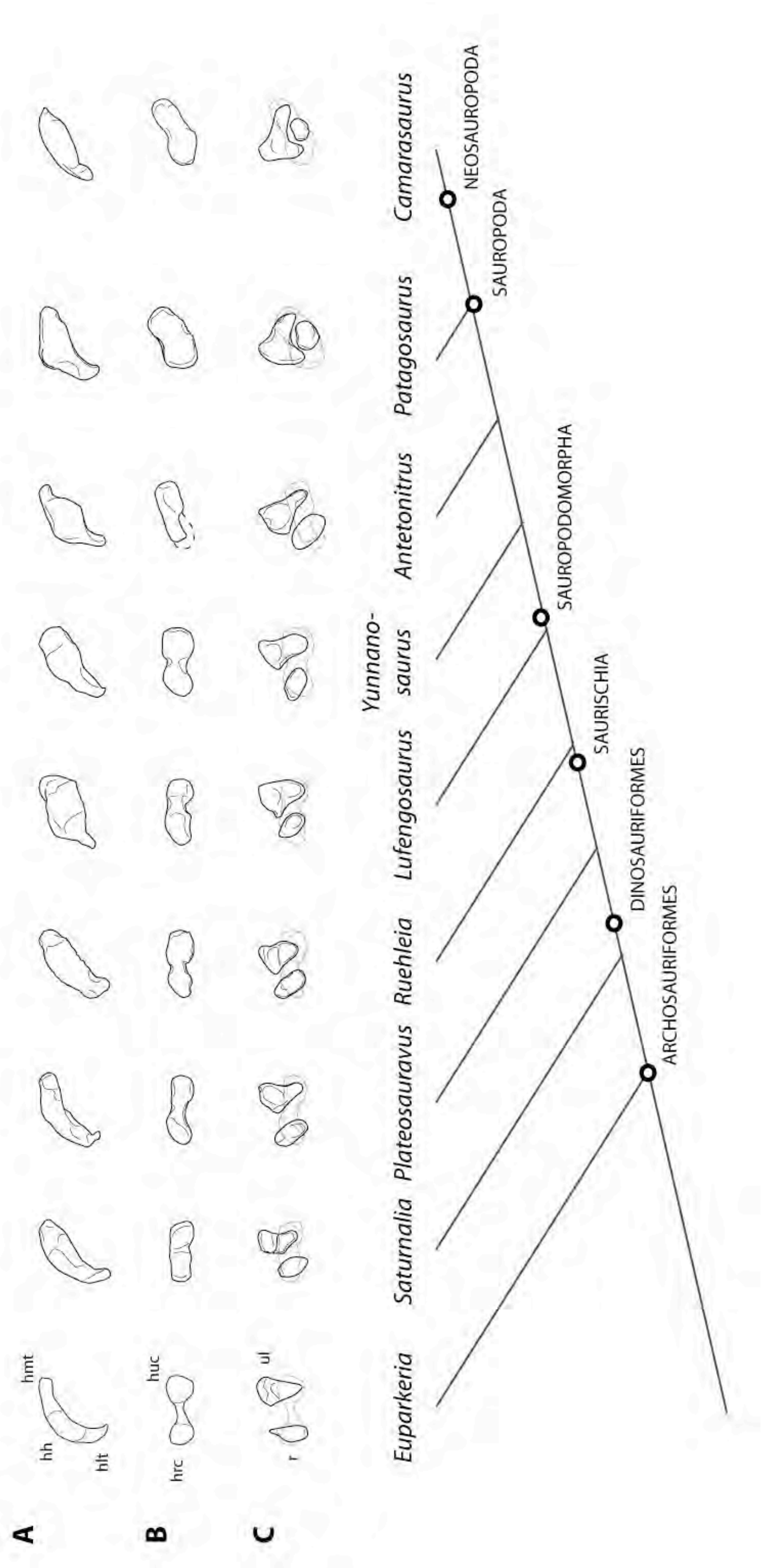

Figure 9-9. Cladogram of the transformations in the humeral joints on the line to neosauropods. **A**, humeral head in proximal view. **B**, distal humeral condyles in distal view, mirrored to bring the radial condyle below the lateral tubercle in row A. **C**, radius and ulna in proximal view with the outline of the distal end of the humerus superposed, showing the natural articulation.

Basal sauropodomorphs retained the plesiomorphic configuration of the distal end of the humerus (fig. 9-9), with clearly separated radial and ulnar condyles (one exception is *Plateosaurus*, see chapter 7). In combination with a semi-erect posture of the humerus, which places the radial condyle craniolateral to the ulnar condyle, partial pronation of the manus was probably possible in most basal sauropodomorphs. In large forms that probably acquired habitual quadrupedality, pronation is additionally aided by a specialized form of the radius (*Lufengosaurus*), or by modified antebrachial muscles (*Yunnanosaurus*) (chapter 7). Effective, permanent pronation of the manus in combination with a more erectly held limb was only possible by two modifications: First, the reduction of the outward twist of the distal humeral expansion, which keeps the radius craniolateral to the ulna despite the more vertical posture of the humerus. Second, the cranial rotation of the radius accompanied by a lateral rotation of the ulna, which further increases the grade of pronation of the manus. The beginnings of both processes are visible in *Antetonitrus* (fig. 9-9B,C), although the radial condyle of the humerus is missing in that taxon and the exact position of the radius cannot be reconstructed. Unfortunately, the lack of good data from the Lower Jurassic prevents monitoring of this character complex (chapter 8): The neosauropod configuration is almost fully developed in the basal eusauropod *Patagosaurus* (fig. 9-9).

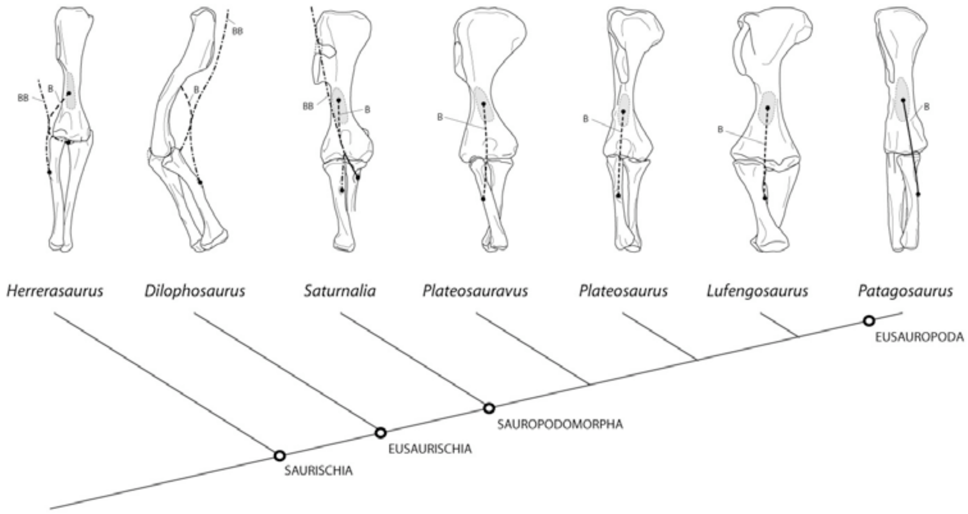

Figure 9-10. Cladogram of different adaptations for manus pronation within Sauropodomorpha. Note that non-sauropod saurischians are shown in ventromedial view, which comes up to a craniomedial view in *Patagosaurus*. *Dilophosaurus* is shown in lateral view.

Antebrachium

As shown in chapters 6 to 8, the evolutionary changes of the shafts and distal ends of radius and ulna are minor. Basal theropods and *Herrerasaurus* retain a plesiomorphic radius to humerus length ratio of about 0.84, a value that is identical to that of *Euparkeria*. In *Eoraptor*, the antebrachium is shortened to a ratio of 0.73, and sauropodomorphs acquire a ratio of about 0.62. Such a relatively low ratio is retained throughout the entire sauropodomorph evolution, and increases only slightly in sauropods (Mauersberger, 2005; fig. 9-10).

Simultaneously, no clear trend in the osteological evolution of the antebrachium can be recognized, with the exception of the reconfiguration of the elbow joint described above. A distinct olecranon process is ossified in *Herrerasaurus*, basal theropods, and *Saturnalia*, but this is not the case in *Euparkeria, Eoraptor,* and all other sauropodomorphs. As described in chapter 7, some genera show specializations in the radius, e.g. a lateral shift of the cranial tubercle, or a oblique course of the shaft relative to the planes of the proximal and distal ends, which may both be interpreted as adaptations to pronate the manus (fig. 9-10). However, these systems cannot be recognized in *Antetonitrus* and higher sauropods, which have evolved a unique solution for the problem of manus pronation (see above, section ‘Elbow joint’). Sauropods have considerably reduced the robustness of radius and ulna relative to their closest outgroup taxa, but resemble early sauropodomorphs like *Plateosauravus* in this respect.

Manus

Momentarily, the evolution of the sauropodomorph manus remains poorly understood. Only a few taxa preserve hands, and these appear specifically adapted in each taxon, possibly indicating ecological specializations. No modifications of the hand musculature can be recognized by the method applied throughout this thesis, but judging from morphology, it can be assumed that the reduction of the digits and tubular arrangement of the metacarpus led to a reduction of the flexor and extensor musculature in eusauropods.

Carpus. As demonstrated by the anatomy of *Heterodontosaurus*, the dinosaurian hand originally retained a plesiomorphic carpus, resembling the basic pattern of all amniotes. Ulnare and intermedium are fused, but a centrale, five distal carpals, and a pisiforme are preserved. In *Herrerasaurus*, the centrale is lost, but the pisiforme and all distal carpals are retained, distal carpal 5 probably being fused to distal carpal 4. Moreover, the radiale is enlarged, while the ulnare is comparatively small, quite the opposite of the condition found in *Heterodontosaurus*. The situation in *Eoraptor* is not entirely clear, since the matrix proximal to metacarpals IV and V is broken away. However, like in other basal dinosaurs, distal carpals 1 to 3 are equally sized and do not extend beyond the proximal surface of their respective metacarpal. The proximal carpals of *Eoraptor* are about equal in size. Basal theropods exhibit a similar morphology, with disc-like radiale and ulnare, and four distal carpals (Colbert, 1989). Thus, the plesiomorphic eusaurischian carpus may be reconstructed as containing ossified radiale and ulnare, and at least four distal carpals that cap metacarpals I–IV.

In sauropodomorphs, the proximal carpals became unossified. One might speculate that this led to a shift of the insertion of M. extensor carpi radialis onto the distal radius, forming a distinct tubercle on its cranial side (chapters 6–8). Nevertheless, distal carpals 1 to 3 are retained in the basal-most sauropodomorphs (*Thecodontosaurus*; Benton et al., 2000). Distal carpal 1 remains ossified in all sauropodomorphs, but the outer distal carpals show a trend towards reduction. However, this trend is broken by the unusual morphology of the carpus of *Jingshanosaurus* (chapter 7). No carpals are known from the fully articulated manus of *Melanorosaurus* (Bonnan and Yates, 2007), but *Shunosaurus* again has at least three disk-like distal carpals, with number 3 somewhat reduced in size (Zhang, 1988; chapter 8). Finally, mamenchisaurids and neosauropods tend to reduce the number of carpals, once more beginning with the outer carpals first. In summary, the pattern of ossifications in the distal carpus of sauropodomorphs is highly fluctuating, but there is a certain resemblance between the carpal morphology of the basal sauropod *Shunosaurus,* and the plesiomorphic condition as observed in *Eoraptor* and *Thecodontosaurus*.

Metacarpus and digits. *Eoraptor* exhibits the most plesiomorphic metacarpus within Dinosauria, with only slightly reduced metacarpals IV and V (chapter 5). An asymmetric metacarpal I is plesiomorphic for dinosaurs, since it is found in *Heterodontosaurus*, *Eoraptor*, *Herrerasaurus*, basal theropods, and sauropodomorphs. In all non-eusauropod sauropodomorphs, metacarpal I is significantly more robustly developed than the remaining metacarpals. The outer metacarpals, as well as the digits, are plesiomorphically slender (even more so than in *Eoraptor*), but become increasingly shorter and more robust in *Massospondylus* and more derived sauropodomorphs (chapter 7).

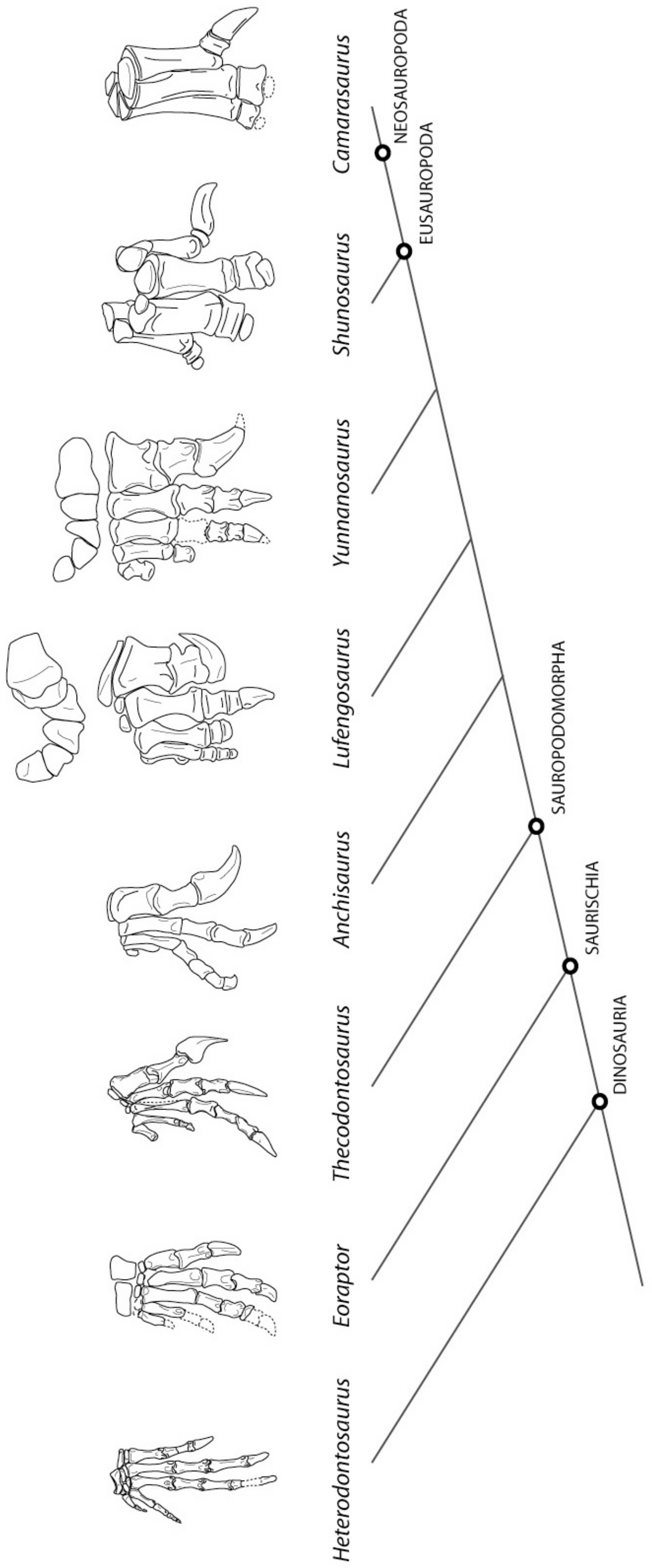

Figure 9-11. Cladogram of manus evolution on the line to neosauropods. In non-sauropod dinosaurs, dorsal views; in sauropods, cranioproximal views. In *Lufengosaurus* and *Yunnanosaurus*, additionally a cranial view of the carpus is provided.

With the evolution of a semitubular metacarpus in *Shunosaurus* (Upchurch, 1994, 1998) and other eusauropods (Monbaron et al., 1999; but see Alifanov and Averianov, 2003), the trend towards shortening of the metacarpals is reversed, and these elements become gradually more elongate in neosauropods. Momentarily, it is not clear when the first steps towards a semitubular metacarpus occurred: *Shunosaurus* already had arranged its metacarpals in a circle segment of about 200° (Upchurch, 1994, 1998; chapter 8), but *Melanorosaurus* (Bonnan and Yates, 2007) and *Yunnanosaurus* show no signs of a considerably curved metacarpus. However, the metacarpus of *Lufengosaurus huenei* (not *L. magnus*) exhibits a distinct curvature of about 140° (chapter 7; fig. 9-11), which, according to current phylogenetic hypotheses, probably reflects parallelism to sauropods.

The phalangeal formula of *Eoraptor* cannot be reconstructed reliably, but was probably similar to other basal dinosaurs such as *Heterodontosaurus,* which counts 2-3-4-3-2. The same phalangeal formula is found in *Plateosaurus*. Within basal sauropodomorphs, digits IV and V tend to be reduced in size and phalangeal count, but retain at least two phalanges in *Massospondylus* and *Lufengosaurus*. *Massospondylus* and more derived sauropodomorphs also evolved the 'prosauropod' manual type 2, with robust metacarpals, a metacarpal I that is wider than long, and short, block-like phalanges. Phalanx V.2 is probably lost in *Melanorosaurus* and more derived sauropodomorphs. With the advent of the semitubular, vertically held metacarpus in eusauropods, the number of phalanges in the cranial digits (II and III) is reduced to 2, with the unguals of all digits except digit I being only rudimentarily developed. In neosauropods, this trend towards reduction of the phalanges is continued, leading to a complete loss of ossified manual digits in titanosaurs (see Upchurch et al., 2004).

Conclusions

This analysis of the evolution of the osteology, myology and functional morphology in sauropodomorphs finds no evidence for *secondary* quadrupedalism in sauropods. Although some basal sauropodomorphs seem to have developed obligate bipedalism (*Plateosaurus*), most forms retained the capability of quadrupedal locomotion, albeit with a plesiomorphical, semi-sprawling posture, the humerus being abducted about 20–30° from the vertical. In this way, 'prosauropods' parallel other large quadrupedal dinosaurs, e.g. ceratopsians (Johnson and Ostrom, 1995; Chapman, 2001; Thompson and Holmes, 2007). Only sauropods evolved an erect humerus that during locomotion swung in parasagittal direction. This was made possible by gradual transformations of the ventral pectoral girdle and elbow joint. Aside from manifold morphological evidence, this result is also supported by rare trackways of basal sauropodomorphs, which demonstrate that 'prosauropod' manus prints are placed distinctly laterally to the pes prints, despite a transversely narrow pectoral girdle and relatively short arms (fig. 9-12). Therefore, the original ideas of Charig et al. (1965) and Galton (1971, 1973, 1976), who described 'prosauropods' as slow habitual quadrupeds that only rarely walked or run bipedally (e.g., in escape), are supported by this analysis.

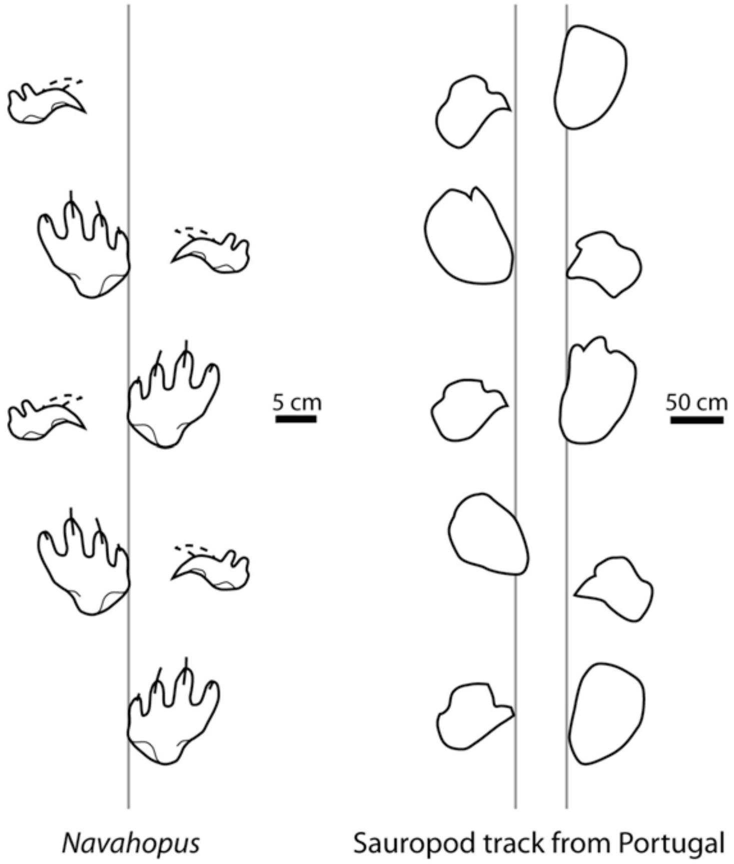

Figure 9-12. Comparison of 'prosauropod' and sauropod tracks. Left, *Navahopus* from the Lower Jurassic of Arizona, USA. After Baird (1980), who identified *Anchisaurus* as the trackmaker of *Navahopus*. Right, Sauropod trackway from the Middle Jurassic of Portugal. After dos Santos et al. (1994).

Clear adaptations to obligate bipedality are also missing in the forelimbs of the basal saurischian *Eoraptor*, but the information about basal dinosauriforms is insufficient. However, the only basal dinosauriform that preserves a rather complete forelimb, *Silesaurus opolensis*, is clearly quadrupedal (Dzik, 2003). Thus, doubts are evoked about the idea of plesiomorphically obligate bipedal dinosaurs (Sereno, 1991, 1997; Carrano, 1999), and it appears more parsimonious that obligate bipedalism was developed only in *Herrerasaurus*, theropods, and ornithopods (see also Fechner, in prep.). Hopefully, future discoveries of basal saurischians and ornithischians from Ladinian and Carnian sediments will help to understand the early evolution of dinosaur locomotion in more detail.

Concerning the evolution within Sauropodomorpha, the transformations from basal sauropodomorphs to eusauropods cannot be traced in all details, due to an incomplete fossil record and a series of autapomorphic developments in the 'prosauropod' taxa that are currently regarded as most closely related to sauropods. Several reoccurrences of seemingly plesiomorphic characters in sauropod forelimbs support the idea that paedomorphism may have played a crucial role in the evolution of this group (see also Reisz et al., 2006). However, most well known 'prosauropods' date much younger than the basal sauropodomorph radiation during the Carnian, which illustrates the probability of both autapomorphic and homoplastic developments with respect to sauropods.

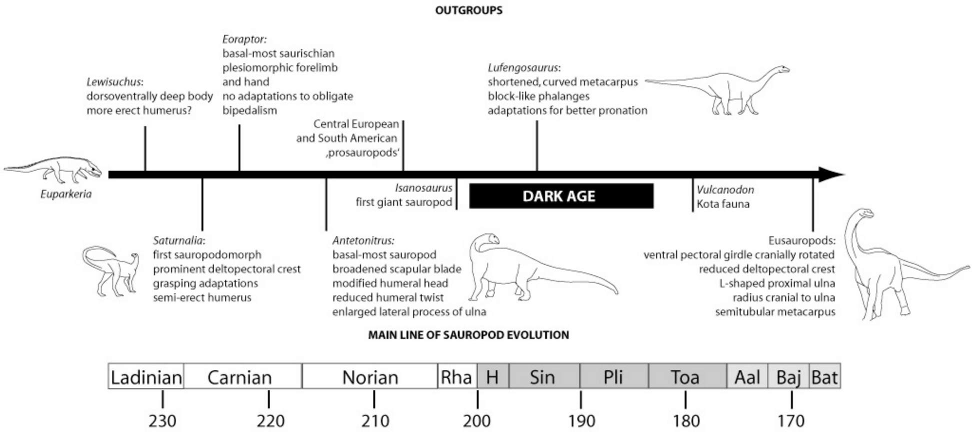

Figure 9-13. Temporal diagram of stages in sauropodomorph forelimb evolution (selection). The large gap in the sauropod fossil record during the Lower Jurassic is illustrated as the 'Dark Age' of sauropod evolution.

Nevertheless, it becomes evident that relatively simple modifications of the basal archosaurian *bauplan* were sufficient to create the sauropod forelimb structure. The key adaptation is the cranial rotation of the ventral shoulder girdle, leading to a ventral orientation of the glenoid and enabling a more erect posture of the humerus. As a consequence, the structure of the elbow joint and the arrangement of radius and ulna had to be reconfigured in order to pronate the hand. Altered lines of action of the deltoid, pectoralis, and supracoracoideus musculature led to a reduction of the deltopectoral crest. However, basal sauropodomorphs and sauropods lack structural or myological novelties in the forelimb that may be regarded as preadaptations for gigantism. On the contrary, the retention of plesiomorphic characters in the forelimb of some basal sauropods (e.g., the scapulocoracoid of *Isanosaurus,* the humerus and antebrachium of *Gongxianosaurus,* and the humerus attributed to *Kotasaurus*) indicates that the optimization of the forelimb posture was a slow, gradual process. Thus, it appears that gigantism and forelimb evolution were parallel, interdependent processes, and not the former a consequence of the latter. The temporal and spatial sequence of these transformations is hard to reconstruct, since the gap in the fossil record between the Early Norian forms (*Melanorosaurus* and *Antetonitrus*) and the Toarcian and Middle Jurassic sauropods is simply too large (fig. 9-13). However, the contemporaneous occurrence of sauropods with different 'grades' of forelimb improvement (e.g., in the Kota and Lower Shaximiao Formations) indicates that the evolution of the neosauropod *bauplan* was a long, complex, and no straightforward process.

10 Summary

This work explores the evolution of the sauropodomorph forelimb in terms of osteological, myological and functional transformations that led to the origin of the sauropod *bauplan*. More than 100 individuals of about 50 fossil taxa of basal archosaurs, basal dinosauriforms, basal saurischians, basal theropods, and sauropodomorphs have been examined in detail in order to identify osteological changes in course of sauropod evolution, including changes in osteological correlates of the musculature. Muscle reconstructions are performed by a modified Extant Phylogenetic Bracket approach: In a first step, all forelimb muscles of extant Reptilia are reviewed in terms of their probable phylogenetic history, nomenclature, and osteological correlates, enabling the inference of the muscular equipment of the last common ancestor of crocodiles and birds. With this knowledge, muscular attachment sites on the pectoral girdle and forelimb are identified in the basal archosaur *Euparkeria*, and gross lines of action of the forelimb muscles are reconstructed. Changes in osteological structures and muscular attachments are then traced along the evolutionary line to sauropods, accompanied by functional interpretations of the modifications observed. This led to the following main results:

- With the exception of the specialized form *Silesaurus*, *Lewisuchus* is the only basal dinosauriform that preserves comparatively good forelimb material. The forelimb of *Marasuchus* has been misidentified and probably belongs to *Hesperosuchus*.
- *Lewisuchus* and *Eoraptor* show no unambiguous adaptations towards obligate bipedality. *Eoraptor* retains a plesiomorphic forelimb anatomy and may well have been able to walk quadrupedally with semi-erect humeri.
- *Herrerasaurus* represents a specialized branch of early saurischians that shows functional parallelism to theropods, but exhibits different osteological and myological adaptations that speak against a close relationship with theropods
- Basal saurischians evolve a unique tubercle cranially on the radius that may be correlated with a specialization of the M. biceps brachii / M. brachialis system that helped to pronate the hand
- Basal sauropodomorphs exhibit a number of modifications that probably correlate with improved maneuverability of the humerus (and there-

fore of the forearm and hand), which enabled effective grasping and manipulation, e.g. of tree branches

- There are no signs of secondary quadrupedalism in sauropods, but most basal sauropodomorphs retained the plesiomorphic ability to walk quadrupedally with semi-erect, partially abducted forelimbs
- Some basal sauropodomorphs evolve unique modifications to effectively pronate the manus for locomotion, which cannot be homologized with the system seen in sauropods
- The key adaptation on the evolutionary line to sauropods is a cranial rotation of the ventral part of the pectoral girdle. This led to a ventral orientation of the glenoid and therefore a vertical posture of the humerus, but the scapular blade keeps being oriented in a plesiomorphic fashion, about 60° to the horizontal plane
- Nonetheless, the relatively conservative construction of the pectoral girdle, with a cranially placed coracoid, largely prevents parasagittal protraction of the humerus in sauropods, hence limiting step length and speed
- Mamenchisaurids, including *Klamelisaurus*, circumvented this constraint by the evolution of a unique shoulder joint that allows the humerus to rotate laterally around the corcacoid for protraction
- The reorientation of the humerus in sauropods led to a number of modifications in the elbow region, including a reduction of the humeral twist, a cranial rotation of the radius, and a lateral shift of the ulna accompanied by the development of an elongate lateral process that articulates with the caudal side of the radial condyle of the humerus. All these modifications at least partially serve to pronate the manus, enabling a reduction of the flexion in the elbow joint during locomotion
- Altered lines of action and therefore functional changes of M. pectoralis, M. supracoracoideus, and M. deltoideus clavicularis, caused by the reorientation of the humerus and ventral pectoral girdle, led to a reduction of the deltopectoral crest
- Due to a large gap in the sauropod fossil record, many evolutionary steps, especially those related to the transformation of the elbow joint and manus, are not preserved
- The optimization of the forelimb towards a fully erect, parasagittally-swinging column was a long evolutionary process, and sauropods seem to have become gigantic prior to the end of this process. Therefore, the

modification of the forelimb was no preadaptation for gigantism, but evolved in parallel.

With these results, this work intends to provide a fundament for future comparisons of archosaurian forelimb evolution, and hopes to inspire others to perform detailed examinations of the proposed functional aspects of sauropod forelimb transformations, e.g. by biomechanical analyses and computer simulations. Lastly, our understanding of the evolution of the sauropods will hopefully be further improved by new discoveries in Upper Triassic and Lower Jurassic strata worldwide.

Acknowledgements

I thank my supervisor, Oliver W. M. Rauhut, and my co-student, Regina Fechner, for their support, for countless fruitful discussions, and for funny beer nights during our research travels. I am especially indebted to Oliver for his kind support and flexibility regarding my lab choice, which was also made possible by the friendly backing of Martin Aberhan, Oliver Hampe and Reinhold Leinfelder. I am very grateful to Martin Sander, the Speaker of the DFG Research Group 533, for the organization of this project and his great support especially during the last phase. Further thanks go to other members of the Research Group for help and discussions, including Andreas Christian, Gordon Dzemski, Bianca Hohn, Dave Hone, Heiner Mallison, Steven Perry, Holger Preuschoft, and Ulrich Witzel. I also thank the staff of the Museum für Naturkunde, Berlin, and of the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, for their aid. My gratitude for granting access to specimens under their custody and for support during collection visits goes to Oscar Alcober, Kumar Ayyasami, Saswati Bandyopadhyay, Bernard Battail, Paul Barrett, José Bonaparte, Jennifer Botha, Matt Carrano, Sandra Chapman, J. Ferigolo, Pat Holroyd, Paul Jeffries, Walter Joyce, Max Langer, Luciano Leal, Heiner Mallison, Li Kui, Liu Jian, Carl Mehling, Mark Norell, Kevin Padian, Jaime Powell, Mike Raath, Charles Schaff, Rainer Schoch, Daniela Schwarz-Wings, Dhurjati Sengupta, Philippe Taquet, Dave Unwin, P. Yadagiri, Adam Yates, Xu Xing, and Zhao Qi. This research was supported by the DFG (German Research Foundation) as part of the Research Unit 533 (grant no. RA 1012/2), by UCMP Doris and Samuel P. Welles Fund, and by EU Synthesys grant FR-TAF 730.

11 Bibliography

ABDALA, V. and MORO, S. 2006. Comparative myology of the forelimb of *Liolaemus* sand lizards (Liolaemidae). Acta Zoologica (Stockholm), **87**, 1-12.

ABEL, O. 1910. Die Rekonstruktion des *Diplodocus*. Abhandlungen der kaiserlichen und königlichen Zoölogisch-Botanischen Gesellschaft in Wien, **5**, 1-60.

ALEXANDER, R. M. 1976. Estimates of speeds of dinosaurs. Nature, **261**, 129-130.

— 1985. Mechanics of posture and gait of some large dinosaurs. Zoological Journal of the Linnean Society, **83**, 1-25.

— 1989. Dynamics of dinosaurs and other extinct giants. Columbia University Press, New York 167 pp.

— and BENNETT, M. B. 1987. Some principles of ligament function, with examples from the tarsal joints of the sheep (*Ovis aries*). Journal of Zoology, **211**, 487-504.

ALIFANOV, V. R. and AVERIANOV, A. O. 2003. *Ferganasaurus verzilini*, gen. et sp. nov., a new neosauropod (Dinosauria, Saurischia, Sauropoda) from the Middle Jurassic of Fergana Valley, Kirghizia. Journal of Vertebrate Paleontology, **23** (2), 358-372.

ALLAIN, R., AQUESBI, N., DEJAX, J., MEYER, C., MONBARON, M., MONTENAT, C., RICHIR, P., ROCHDY, M., RUSSELL, D. and TAQUET, P. 2004. A basal sauropod dinosaur from the Early Jurassic of Morocco. Comptes Rendus Palevol, **3** (3), 199-208.

AN, K. N., TAKAHASHI, T., HARRIGAN, T. P. and CHAO, E. Y. 1984. Determination of muscle orientations and moment arms. Journal of Biomechanic Engineering, **106**, 280-283.

ARCUCCI, A. B. 1997. Dinosauromorpha. 179-184. In CURRIE, P. J. and PADIAN, K. (eds). Encyclopedia of Dinosaurs. Academic Press, San Diego.

BAIRD, D. 1980. A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic) of Arizona. 219-230. In JACOBS, L. L. (eds). Aspects of Vertebrate History. Museum of Northern Arizona Press, Flagstaff.

BAKKER, R. L. 1971. Ecology of the brontosaurs. Nature, **229**, 172-174.

— and GALTON, P. M. 1974. Dinosaur monophyly and a new class of vertebrates. Nature, **248**, 168-172.

BANDYOPADHYAY, S. 1999. Gondwana vertebrate faunas of India. PINSA, **65**, 285-313.

— and ROY-CHOWDHURY, T. 1996. Beginning of the continental Jurassic in India: A paleontological approach. Museum of Northern Arizona Bulletin, **60**, 371-378.

—, — and SENGUPTA, D. P. 2002. Taphonomy of some Gondwana vertebrate assemblages of India. Sedimentary Geology, **147**, 219-245.

BARRETT, P. M. 1999. A sauropod dinosaur from the Lower Lufeng Formation (Lower Jurassic) of Yunnan Province, People's Republic of China. Journal of Vertebrate Paleontology, **19**, 785-787.

— and UPCHURCH, P. 2005. Sauropodomorph diversity through time: Macroevolutionary and paleoecological implications. 125-156. In CURRY ROGERS, K. and WILSON, J. A. (eds). The Sauropods: Evolution and Paleobiology. University of California Press, Berkeley.

— and — 2007. The evolution of feeding mechanisms in early sauropodomorph dinosaurs. Special Papers in Palaeontology, **77**, 91-112.

BAUMEL, J. J. and WITMER, L. M. 1993. Osteologia. 45-132. In BAUMEL, J. J., KING, A. S., BREAZILE, J. E., EVANS, H. E. and VANDEN BERGE, J. C. (eds). Handbook of Avian Anatomy: Nomina Anatomica Avium. Nuttall Ornithological Club, Cambridge.

—, KING, A. S., BREAZILE, J. E., EVANS, H. E. and VANDEN BERGE, J. C. (eds) 1993. Handbook of Avian Anatomy: Nomina Anatomica Avium (second edition). Nuttall Ornithological Club, Cambridge, 779 pp.

de BEER, G. 1956. The evolution of ratites. Bulletin of the British Museum of Natural History, **4**, 59-70.

BELLAIRS, A. D. 1969. The Life of Reptiles. Weidenfeld & Nicolson, London, 615 pp.

— and JENKIN, C. R. 1960. The Skeleton of Birds. 241-299. In MARSHALL, A. J. (eds). Biology and Comparative Physiology of Birds, Volume 1. Academic Press, New York.

BENNETT, S. C. 1996. The phylogenetic position of the Pterosauria within the Archosauromorpha. Zoological Journal of the Linnean Society, **118**, 261-308.

BENTON, M. J. 1984. Fossil reptiles from the German Late Triassic and the origin of the dinosaurs. 13-18. In REIF, W.-E. and WESTPHAL, F. (eds). Third Symposium on Mesozoic Terrestrial Ecosystems, short papers. Attempto Verlag, Tübingen.

— 1990. Origin and interrelationships of dinosaurs. 11-30. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). The Dinosauria. University of California Press, Berkeley.

— 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. Philosophical Transactions of the Royal Society of London Series B Biological Sciences, **354** (1388): 1423-1446.

— 2004. Origin and Relationships of Dinosauria. 7-19. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). The Dinosauria, second edition. University of California Press, Berkeley.

— and CLARK, J. M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. 289-332. In BENTON, M. J. (eds). The Phylogeny and Classification of Tetrapods. Vol. 1, Amphibians, Reptiles, Birds. Clarendon Press, Oxford.

—, JUUL, L., STORRS, G. W. and GALTON, P. M. 2000. Anatomy and systematics of the prosauropod dinosaur *Thecodontosaurus antiquus* from the Upper Triassic of southwest England. Journal of Vertebrate Paleontology, **20** (1), 77-108.

BERGER, A. J. 1953. On the locomotory anatomy of the Blue Coua, *Coua caerulea*. Auk, **70**, 49-83.

— 1954. The myology of the pectoral appendage of three genera of American cuckoos. Miscellaneous Publications of the Museum of Zoology of the University of Michigan, **85**, 1-35.

— 1955. On the anatomy and relationships of Glossy Cuckoos of the genera *Chrysococcyx*, *Lampromorpha*, and *Chalcites*. Proceedings of the U.S. National Museum, **103**, 585-597.

— 1956a. The appendicular myology of the Pygmy Falcon (*Polihierax semitorquatus*). American Midland Naturalist, **55**, 326-333.

— 1956b. The appendicular myology of the Sandhill Crane, with comparative remarks on the Whooping Crane. Wilson Bulletin, **68**, 282-304.

— 1956c. On the anatomy of the Red Bird of Paradise, with comparative remarks on the Corvidae. Auk, **73**, 427-446.

— 1957. On the anatomy and relationships of *Fergilupus varius*, an extinct starling from the Mascarane Islands. Bulletin of the American Museum of Natural History, **113**, 225-272.

— 1960. The musculature. 301-344. In MARSHALL, A. J. (ed). Biology and comparative physiology of birds. 2 vols. Academic Press, New York.

— 1966. The musculature. 224-500. In GEORGE, J. C. and BERGER, A. J. (eds). Avian myology. Academic Press, New York.

BERTRAM, J. E. A. and BIEWENER, A. A. 1988. Bone curvature: sacrificing strength for load predictability? Journal of Theoretical Biology, **131**, 75-92.

— and — 1992. Allometry and curvature in the long bones of quadrupedal mammals. Journal of Zoology, **226**, 455-467.

BIEWENER, A. A. 1989a. Scaling body support in mammals: limb posture and muscle mechanics. Science, **245**, 45-48.

— 1989b. Mammalian terrestrial locomotion and size. Mechanical design principles define limits. BioScience, **39**, 776-783.

— 1990. Biomechanics of mammalian terrestrial locomotion. Science, **250**, 1097-1103.

— 1991. Musculoskeletal design in relation to body size. Journal of Biomechanics, **24** (Supplement 1), 19-30.

BOCK, W. J. 1968. Mechanics of one- and two-joint muscles. American Museum Novitates, **2319**, 1-45.

BONAPARTE, J. F. 1969. Dos nuevas "faunas" de reptiles Triásicos de Argentina. I. Gondwana Symposium, Mar del Plata. Ciencias Tierra, 2, 283-306.

— 1971. Los tetrapodos del sector Superior de la Formacion Los Colorados, La Rioja, Argentina (Triásico Superior). I Parte. Opera Lilloana, **22**, 1-183.

— 1975. Nuevos materiales de *Lagosuchus talampayensis* Romer (Thecodontia-Pseudosuchia) y su significado en el origin de los Saurischia. Chañarense inferior, Triásico Medio de Argentina. Acta Geologica Lilloana, **13**, 5-90.

— 1979. Dinosaurs: a Jurassic assemblage from Patagonia. Science, **205**, 1377-1379.

— 1986a. Les Dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du Jurassique moyen de Cerro Cóndor (Chubut, Argentine). Annales de Paleontologie, **72**, 247-289, 326-386.

— 1986b. The early radiation and phylogenetic relationships of the Jurassic sauropod dinosaurs, based on vertebral anatomy. 245-258. In PADIAN, K. (ed). The Beginning of the Age of Dinosaurs. Cambridge University Press, Cambridge.

— 1999. Evolución de las vértebras presacras en Sauropodomorpha. Ameghiniana, **36**, 115-187.

— and VINCE, M. 1979. El hallazgo del primer nido de dinosaurios triásicos (Saurischia, Prosauropoda), Triásico superior de Patagonia, Argentina. Ameghiniana, **16** (1-2), 173-182.

—, FERIGOLO, J. and RIBERIO, A. M. 1999. A new early Late Triassic saurischian dinosaur from Rio Grande do Sul State, Brazil. 89-109. In TOMIDA, Y., RICH, T. H. and VICKERS-RICH, P. (eds). Proceedings of the Second Gondwanan Dinosaur Symposium. National Science Museum Monographs, Tokyo.

—, BREA, G., SCHULTZ, C. L. and MARTINELLI, A. G. 2007. A new specimen of *Guaibasaurus candelariensis* (basal Saurischia) from the Late Triassic Caturrita Formation of southern Brazil. Historical Biology, **19**, 73-82.

BONNAN, M. F. 2001. The evolution and functional morphology of sauropod dinosaur locomotion. PhD Dissertation, Northern Illinois University, 700 pp.

— 2003. The evolution of manus shape in sauropod dinosaurs: Implications for functional morphology, forelimb orientation, and phylogeny. Journal of Vertebrate Paleontology, **23** (3), 595-613.

— 2004. Morphometric analysis of humerus and femur shape in Morrison sauropods: implications for functional morphology and paleobiology. Paleobiology, **30** (3), 444-470.

— 2005. Pes anatomy in sauropod dinosaurs: implications for functional morphology, evolution, and phylogeny. 346-380. In TIDWELL, V. and CARPENTER, K. (eds). Thunder-Lizards: The Sauropodomorph Dinosaurs. Indiana University Press, Bloomington.

— and SENTER, P. 2007. Were the basal sauropodomorph dinosaurs *Plateosaurus* and *Massospondylus* habitual quadrupeds? Special Papers in Palaeontology, **77**, 139-155.

— and YATES, A. M. 2006. The forelimb of the basal sauropodomorph *Melanorosaurus* and the evolution of pronation, manus shape, and quadrupedalism in sauropods. Journal of Vertebrate Paleontology, **26** (supplement to No. 3), 44A.

— and — 2007. A new description of the forelimb of the basal sauropodomorph *Melanorosaurus*: implications for the evolution of pronation, manus shape and quadrupedalism in sauropod dinosaurs. Special Papers in Palaeontology, **77**, 157-168.

BRINKMAN, D. B. and SUES, H. D. 1987. A staurikosaurid dinosaur from the Upper Triassic Ischigualasto Formation of Argentina and the relationships of the Staurikosauridae. Palaeontology, **30**, 493-503.

BRISTOWE, A. and RAATH, M. A. 2004. A juvenile coelophysoid skull from the Early Jurassic of Zimbabwe, and the synonymy of *Coelophysis* and *Syntarsus*. Palaeontologia Africana, **40**, 31-41.

BROOM, R. 1911. On the dinosaurs of the Stromberg, South Africa. Annals of the South Africa Museum, **7**, 291-308.

— 1913a. Note on *Mesosuchus browni* Watson, and on a new South-African Triassic Pseudosuchian (*Euparkeria capensis*). Records of the Albany Museum, **2** (5), 394.

— 1913b. On the South African pseudosuchian *Euparkeria* and allied genera. Proceedings of the Zoological Society London, **1913**, 619-633.

BRYANT, H. N. and RUSSELL, A. P. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, **337**, 405-418.

— and — 1993. The occurrence of clavicles within Dinosauria: implications for the homology of the avian furcula and the utility of negative evidence. Journal of Vertebrate Paleontology, **13**, 171-184.

— and SEYMOUR, K. L. 1990. Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. Journal of Morphology, **206**, 109-117.

BUFFETAUT, E. 2005. A new sauropod dinosaur with prosauropod-like teeth from the Middle Jurassic of Madagascar. Bulletin de la Societe Geologique de France, **176** (5), 467-473.

—, SUTEETHORN, V., CUNY, G., TONG, H., LE LOEUFF, J., KHANSUBHA, S. and JONGAUTCHARLYAKUL, S. 2000. The earliest known sauropod dinosaur. Nature, **407** (6800), 72-74.

—, —, LE LOEUFF, J., CUNY, G., TONG, H. and KHANSUBHA, S. 2002. The first giant dinosaurs: a large sauropod form the Late Triassic of Thailand. Comptes Rendus Palevol, **1**, 103-109.

BURNESS, G. P., DIAMOND, J. and FLANNERY, T. 2001. Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. Proceedings of the National Academy of Sciences, **98** (25), 14518-14523.

BUTLER, R. J., UPCHURCH, P. and NORMAN, D. B. 2007a. The phylogeny of the ornithischian dinosaurs. Journal of Systematic Palaeontology, **5** (4), 1-40.

—, SMITH, R. M. H. and NORMAN, D. B. 2007b. A primitive ornithischian dinosaur from the Late Triassic of South Africa, and the early evolution and diversification of Ornithischia. Proceedings of the Royal Society B: Biological Sciences, **274** (1621), 2041-2046.

BYERLY, T. C. 1925. The myology of *Sphenodon punctatum*. University of Iowa Studies in Natural History, **11**, 3-51.

CALVO, J. O. and SALGADO, L. 1995. *Rebbachisaurus tessonei* sp. nov. a new Sauropoda from the Albain-Cenomanian of Argentina; new evidence on the origin of the Diplodocidae. GAIA, **11**, 13-33.

CAMP, C. L. 1936. A new type of small bipedal dinosaur from the Navajo Sandstone of Arizona. University of California Publications in Geological Sciences, **24**, 39-56.

CARPENTER, K. 2002. Forelimb biomechanics of nonavian theropod dinosaurs in predation. Senckenbergiana lethaea, **82** (1), 59-76.

— and SMITH, M. 2001. Forelimb osteology and biomechanics of *Tyrannosaurus rex*. 90-116. In TANKE, D. and CARPENTER, K. (eds). Mesozoic Vertebrate Life. Indiana University Press, Bloomington.

CARRANO, M. T. 1999. What, if anything, is a cursor? Categories versus continua for determining locomotor habit in mammals and dinosaurs. Journal of Zoology London, **247**, 29-42.

— 2000. Homoplasy and the evolution of dinosaur locomotion. Paleobiology, **26** (3), 489-512.

— 2005. The evolution of sauropod locomotion: Morphological diversity of a secondarily quadrupedal radiation. 229-251. In CURRY ROGERS, K. and WILSON, J. A. (eds). The Sauropods: Evolution and Paleobiology. University of California Press, Berkeley.

—, HUTCHINSON, J. R. and SAMPSON, S. D. 2005. New information on *Segisaurus halli*, a small theropod dinosaur from the Early Jurassic of Arizona. Journal of Vertebrate Paleontology, **25**, 835-849.

CARTER, D. R., MIKIC, B. and PADIAN, K. 1998. Epigenetic mechanical factors in the evolution of long bone epiphyses. Zoological Journal of the Linnean Society, **123**, 163-178.

CASAMIQUELA, R. M. 1967. Un nuevo dinosaurio ornitischio Triásico (*Pisanosaurus mertii*: Ornithopoda) de la Formación Ischigualasto, Argentina. Ameghiniana, **4**, 47-64.

— 1977. The presence of the genus *Plateosaurus* (Sauropodomorpha) in the Upper Triassic of the El Tranquillo Formation, Patagonia. 30-31. In (eds). 4th International Gondwana Symposium, Abstracts.

— 1980. La presencia del genero *Plateosaurus* (Prosauropoda) en el Triásico superior de la Formación El Tranquilo, Patagonia. Actas II Congreso Argentino de Paleontologia y Bioestratigrafia, I Congreso Latinoamericano de Paleontolgia, Buenos Aires, 2-6 April 1980, **1**, 143-158.

CHAPMAN, R. 2001. A new posture of the horned dinosaur *Triceratops*. Journal of Vertebrate Paleontology, **21** (Supplement to No. 3), 39A.

CHARIG, A. J., ATTRIDGE, J. and CROMPTON, A. W. 1965. On the origin of the sauropods and the classification of the Saurischia. Proceedings of the Linnean Society of London, **176**, 197-221.

CHEN, H. K. 1935. Development of the pectoral limb of *Necturus maculosus*. Illinois Biological Monographs, **14** (1), 1-71.

CHIAPPE, L. M., JACKSON, F., CORIA, R. A. and DINGUS, L. 2005. Nesting titanosaurs from Auca Mahuevo and adjacent sites: Understanding sauropod reproductive behavior and embryonic development. 285-302. In CURRY ROGERS,

K. and WILSON, J. A. (eds). The Sauropods: Evolution and Paleobiology. University of California Press, Berkeley.

CHRISTIAN, A. 2002. Neck posture and overall body design in sauropods. Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe, **5**, 271-281.

— and DZEMSKI, G. 2007. Reconstruction of the cervical skeleton posture of *Brachiosaurus brancai* Janensch, 1914 by an analysis of the intervertebral stress along the neck and a comparison with the results of different approaches. Fossil Record, **10** (1), 38-49.

— and HEINRICH, W.-D. 1998. The neck posture of *Brachiosaurus brancai*. Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe, **1**, 73-80.

— and PREUSCHOFT, H. 1996. Deducing the body posture of extinct large vertebrates from the shape of the vertebral column. Palaeontology, **39** (4), 801-812.

—, HEINRICH, W.-D. and GOLDER, W. 1999a. Posture and mechanics of the forelimbs of *Brachiosaurus brancai* (Dinosauria: Sauropoda). Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe, **2**, 63-73.

—, MÜLLER, R. H. G., CHRISTIAN, G. and PREUSCHOFT, H. 1999b. Limb swinging in elephants and giraffes and implications for the reconstruction of limb movements and speed estimates in large dinosaurs. Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe, **2**, 81-90.

CHRISTIANSEN, P. 1997a. Locomotion in sauropod dinosaurs. GAIA, **14**, 45-75.

— 1997b. Forelimbs and Hands. 245-253. In CURRIE, P. J. and PADIAN, K. (eds). Encyclopedia of Dinosaurs. Academic Press, San Diego.

— 1999. On the head size of sauropodomorph dinosaurs: Implications for ecology and physiology. Historical Biology, **13** (4), 269-297.

— 2000. Feeding mechanisms of the sauropod dinosaurs *Brachiosaurus*, *Camarasaurus*, *Diplodocus*, and *Dicraeosaurus*. Historical Biology, **14** (3), 137-152.

CHURE, D. L. and MADSEN, J. H. 1996. On the presence of furculae in some non-maniraptoran theropods. Journal of Vertebrate Paleontology, **16**, 573-577.

CLARK, J. M., SUES, H.-D. and BERMAN, D. S. 2000. A new specimen of *Hesperosuchus agilis* from the Upper Triassic of New Mexico and the interrelationships of basal crocodylomorph archosaurs. Journal of Vertebrate Paleontology, **20** (4), 683-704.

—, XU, X., FORSTER, C. A. and WANG, Y. 2004. A Middle Jurassic 'sphenosuchian' from China and the origin of the crocodylian skull. Nature, **430**, 1021-1024.

CLUVER, M. A. 1978. Fossil Reptiles of the South African Karoo. South African Museum, Cape Town, 54 pp.

COLBERT, E. H. 1962. The weights of dinosaurs. American Museum Novitates, **2076**, 1-16.

— 1964. Relationships of the saurischian dinosaurs. American Museum Novitates, **2181**, 1-24.

— 1970. A saurischian dinosaur from the Triassic of Brasil. American Museum of Arizona Bulletin, **57**, 1-60.

— 1989. The Triassic dinosaur *Coelophysis*. Museum of Northern Arizona Bulletin, **57**, 1-160.

— 1997. North American Dinosaur Hunters. In J. O. Farlow and M. K. Brett-Surman (eds). The complete dinosaur. Indiana University Press, Bloomington, 24-33 pp.

CONG, L., HOU, L.-H. and WU, X. C. 1998. The gross anatomy of *Alligator sinensis* Fauvel. CIP, Beijing, 388 pp.

COOMBS, W. P. J. 1975. Sauropod habits and habitats. Palaeogeography, Palaeoclimatology, Palaeoecology, **17**, 1-33.

— 1978a. Theoretical aspects of cursorial adaptation in dinosaurs. Quarterly Review of Biology, **53**, 393-418.

— 1978b. Forelimb muscles of the Ankylosauria (Reptilia: Ornithischia). Journal of Paleontology, **52**, 642-657.

COOPER, M. R. 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. Occasional Papers of the National Museum of Rhodesia, Series B Natural Sciences, **6** (10), 689-840.

— 1984. A reassessment of *Vulcanodon karibaensis* RAATH (Dinosauria: Saurischia) and the origin of the Sauropoda. Palaeontologia Africana, **25**, 203-231.

COPE, E. D. 1867. An account of extinct reptiles that approach birds. Proceedings of the Academy of Natural Sciences of Philadelphia, **19**, 234-235.

— 1878a. On some saurians found in the Triassic of Pennsylvania, by C. M. Wheatley. Proceedings of the American Philosophical Society, **17**, 231-232.

— 1878b. On the Vertebrata of the Dakota Epoch of Colorado. Proceedings of the American Philosophical Society, **17**, 233-247.

— 1878c. On the saurians recently discovered in the Dakota Beds of Colorado. American Naturalist, **12**, 71-85.

— 1878d. On the saurians of the Dakota Cretaceous rocks of Colorado. Nature, **18**, 476.

CRACRAFT, J. 1974. Phylogeny and evolution of ratite birds. Ibis, **116**, 494-521.

CRUICKSHANK, A. R. I. 1975. The origin of sauropod dinosaurs. South African Journal of Science, **71**, 89-90.

CRUSH, P. J. 1984. A late Upper Triassic sphenosuchid crocodilian from Wales. Palaeontology, **27** (1), 131-157.

CUBO, J., MENTEN, L. and CASINOS, A. 1999. Sagittal long bone curvature in birds. Annales des Sciences Naturelles, **20** (4), 153-159.

CURRY, K. A. 1999. Ontogenetic histology of *Apatosaurus* (Dinosauria: Sauropoda): new insights on growth rates and longevity. Journal of Vertebrate Paleontology, **19** (4), 654-665.

CURRY ROGERS, K. and ERICKSON, G. M. 2005. Sauropod histology: Microscopic views on the lives of giants. 303-326. In CURRY ROGERS, K. and WILSON, J. A. (eds). The Sauropods: Evolution and Paleobiology. University of California Press, Berkeley.

— and FORSTER, C. A. 2001. The last of the dinosaur titans: a new sauropod from Madagascar. Nature, **412**, 530-534.

DANIELS, C. B. and PRATT, J. 1992. Breathing in long necked dinosaurs: Did the sauropods have bird lungs? Comparative Biochemistry and Physiology, **101 (A)**, 43-46.

DAVIS, D. D. 1936. The terminology of reptilian musculature. Herpetologica, **1**, 12-17.

DILKES, D. W. 2000. Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. Transactions of the Royal Society of Edinburgh Earth Sciences, **90** (2), 87-125.

DODSON, P. 1990. Sauropodomorpha. 318-319. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). The Dinosauria. University of California Press, Berkeley.

DOLGO-SABUROFF, B. 1929. Über Ursprung und Insertion der Skelettmuskeln. Anatomischer Anzeiger, **68**, 80-87.

DOLLO, L. 1906. Les dinosauriens adaptés a la vie quadrupède secondaire. Memoires de la Société belge de la Géologie, **19**, 441-448.

DONG, Z. 1984. [A new prosauropod from Ziliujing Formation of Sichuan Basin]. Vertebrata PalAsiatica, **22**, 310-313.

— and TANG, Z. 1984. [Note on a new Mid-Jurassic sauropod (*Datousaurus bashanensis* gen. et sp. nov.) from Sichuan Basin, China]. Vertebrata PalAsiatica, **22**, 69-74.

—, ZHOU, S. and ZHANG, Y. 1983. The dinosaurian remains from Sichuan Basin, China. Palaeontologica Sinica, **162**, 1-145.

DOWNS, A. 2000. *Coelophysis bauri* and *Syntarsus rhodesiensis* compared, with comments on the preparation and preservation of the fossils from the Ghost Ranch *Coelophysis* Quarry. New Mexico Museum of Natural History and Science Bulletin, **17**, 33-38.

DUNCAN, R. A., HOOPER, P. R., REHACEK, J., MARSH, J. S. and DUNCAN, A. R. 1997. The timing and duration of the Karoo igneous event, southern Gondwana. Journal of Geophysical Research, **102** (B8), 18127-18138.

DYLEVSKY, I. 1968. Muscles of intermetacarpal spatium in the bird wing development and homology. Folia morphologia (Prague), **16**, 277-285.

DZIK, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. Journal of Vertebrate Paleontology, **23** (3), 556-574.

EWER, R. F. 1965. The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Philosophical Transactions of the Royal Society of London Series B Biological Sciences, **248**, 379-435.

FARLOW, J. O., DODSON, P. and CHINSAMY, A. 1995. Dinosaur biology. Annual Reviews of Ecology and Systematics, **26**, 445-471.

—, GATESY, S. M., HOLTZ, T. R. Jr., HUTCHINSON, J. R. and ROBINSON, J. M. 2000. Theropod locomotion. American Zoologist, **40**, 640-663.

FEDAK, T. J. and GALTON, P. M. 2007. New information on the braincase and skull of *Anchisaurus polyzelsus* (Lower Jurassic, Connecticut, USA; Saurischia: Sauropodomorpha): implications for sauropodomorph systematics. Special Papers in Palaeontology, **77**, 245-260.

FEDUCCIA, A. 1986. The scapulocoracoid of flightless birds: a primitive avian character similar to that of theropods. Ibis, **128**, 128-132.

FISHER, H. J. 1946. Adaptations and comparative anatomy of the locomotor apparatus of New World Vultures. American Midland Naturalist, **35**, 545-727.

— and GOODMAN, D. C. 1955. The myology of the Whooping Crane, *Grus americana*. Illinois Biological Monographs, **24**, 1-127.

FRANCIS, E. T. B. 1934. The anatomy of the salamander. Clarendon Press, Oxford, 381 pp.

FRASER, N. C., PADIAN, K., WALKDEN, G. M. and DAVIS, A. L. M. 2002. Basal dinosauriform remains from Britain and the diagnosis of the Dinosauria. Palaeontology, **45** (1), 79-95.

FROST, H. M. 1990. Skeletal structural adaptations to mechanical usage (SATMU). Anatomical Record, **226**, 403-439.

FUJIOKA, T. 1959. Vergleichende und topographische Anatomie des Geflügels. 1. Mitteilungen über die Ursprünge und die Ansätze der Muskeln der Schulterextremität des Geflügels. Japanese Journal of Veterinary Science, **21**, 85-95.

FÜRBRINGER, M. 1876. Zur vergleichenden Anatomie der Schultermuskeln - 3. Teil, Capitel IV: Saurier und Crocodile. Gegenbaurs Morphologisches Jahrbuch, **1**, 636-816.

— 1886. Über Deutung und Nomenklatur der Muskulatur des Vogelflügels.

Morphologisches Jahrbuch, **2**, 121-125.

— 1888. Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane. T. van Jolkema, Amsterdam, 40 pp.

— 1900. Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln, IV. Teil: Reptilien. Jenaische Zeitschrift für Naturwissenschaft, **34**, 215-712.

— 1902. Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln, V. Teil: Vögel. Jenaische Zeitschrift für Naturwissenschaft, **36**, 289-736.

GADOW, H. and SELENKA, E. 1891. Vögel. I. Anatomischer Theil. Dr. H. G. Bronn's Klassen und Ordnungen des Thier-Reichs, **6** (4), 1-1008.

GALTON, P. M. 1971a. The prosauropod dinosaur *Ammosaurus*, the crocodile *Protosuchus*, and their bearing on the age of the Navajo Sandstone of northeastern Arizona. Journal of Paleontology, **45**, 781-795.

— 1971b. Manus movements of the coelurosaurian dinosaur *Syntarsus* and opposability of the theropod hallux (sic.). Arnoldia, **5**, 1-8.

— 1973. On the anatomy and relationships of *Efraasia diagnostica* (v. Huene) n. gen., a prosauropod dinosaur (Reptilia: Saurischia) from the Upper Triassic of Germany. Paläontologische Zeitschrift, **47**, 229-255.

— 1976. Prosauropod dinosaurs (Reptilia: Saurischia) of North America. Postilla, Yale Peabody Museum, **169**, 1-98.

— 1984a. An early prosauropod dinosaur from the upper Triassic of Nordwürttemberg, West Germany. Stuttgarter Beiträge zur Naturkunde, Serie B, **106**, 1-25.

— 1984b. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from the Knollenmergel (Middle Keuper, Upper Triassic) of Germany. I. Two complete skulls from Trossingen/Württemberg with comments on the diet. Geologica et Palaeontologica, **18**, 139-171.

— 1985a. Diet of prosauropod dinosaurs from the late Triassic and early Jurassic. Lethaia, **18**, 105-123.

— 1985b. Cranial anatomy of the prosauropod dinosaur *Sellosaurus gracilis* from the Middle Stubensandstein (Upper Triassic) of Nordwürttemberg, West Germany. Stuttgarter Beiträge zur Naturkunde, Serie B, **118**, 1-39.

— 1990. Basal Sauropodomorpha - Prosauropoda. 320-344. In WEISHAMPEL, D. B., DODSON, P. and OSMOLSKA, H. (eds). The Dinosauria. University of California Press, Berkeley.

— 1997. Comments on sexual dimorphism in the prosauropod dinosaur *Plateosaurus engelhardti* (Upper Triassic, Trossingen). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **1997**, 674-682.

— 1999. Sex, sacra and *Sellosaurus gracilis* (Saurischia, Sauropodomorpha, Upper Triassic, Germany) - or why the character "two sacral vertebrae" is plesiomorphic for Dinosauria. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **213**, 19-55.

— and CLUVER, M. A. 1976. *Anchisaurus capensis* (Broom) and a revision of the Anchisauridae (Reptilia: Saurischia). Annals of the South African Museum, **69**, 121-159.

— and UPCHURCH, P. 2004. Prosauropoda. 232-258. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). The Dinosauria, second edition. University of California Press, Berkeley.

—, van HEERDEN, J. and YATES, A. M. 2005. Postcranial anatomy of referred specimens of the sauropodomorph dinosaur *Melanorosaurus* from the Upper Triassic of South Africa. 1-37. In TIDWELL, V. and CARPENTER, K. (eds). Thunder-Lizards: The Sauropodomorph Dinosaurs. Indiana University Press, Bloomington.

—, YATES, A. M. and KERMACK, D. 2007. *Pantydraco* n. gen. for *Thecodontosaurus caducus* YATES, 2003, a basal sauropodomorph dinosaur from the Upper Triassic or Lower Jurassic of South Wales, UK. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **243** (1), 119-125.

GANS, C. 1988. Muscle insertions do not incur mechanical advantage. Acta Zoologica Cracovia, **31**, 615-624.

— and BOCK, W. J. 1965. The functional significance of muscle architecture, a theoretical analysis. Reviews of Anatomy, Embryology and Cell Biology, **38**, 115-142.

GARDNER, E. 1950. Physiology of movable joints. Physiological Reviews, **30**, 127-176.

GATESY, S. M. 1990. Caudofemoral musculature and the evolution of theropod locomotion. Paleobiology, **16** (2), 170-186.

— 1995. Functional evolution of the hindlimb and tail from basal theropods to birds. 219-234. In THOMASON, J. J. (eds). Functional morphology in vertebrate paleontology. Cambridge University Press, Cambridge.

— 2001. The evolutionary history of the theropod caudal locomotor muscle. 333-347. In GAUTHIER, J. A. and GALL, L. F. (eds). New Perspectives on the Origin and Early Evolution of Birds. Peabody Museum of Natural History, New Haven.

— 2002. Locomotor Evolution on the Line to Modern Birds. 432-447. In CHIAPPE, L. M. and WITMER, L. M. (eds). Mesozoic Birds. University of California Press, Berkeley.

— and BAIER, D. B. 2005. The origin of the avian flight stroke: a kinematic and kinetic perspective. Paleobiology, **31** (3), 382-399.

— and MIDDLETON, K. M. 1997. Bipedalism, flight, and the evolution of theropod locomotor diversity. Journal of Vertebrate Paleontology, **17** (2), 308-329.

GAUFFRE, F.-X. 1995. Phylogeny of prosauropod dinosaurs. Journal of Vertebrate Paleontology, **15** (supplement to No. 3), 31A.

— 1996. Phylogénie des dinosaures prosauropodes et étude d'un prosauropode du Trias supérieur d'Afrique australe. PhD dissertation, 2 vols. Muséum National d'Histoire Naturelle de Paris, Paris, 156 pp.

GAUTHIER, J. A. 1984. A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. dissertation, University of California, Berkeley, 564 pp.

— 1986. Saurischian monophyly and the origin of birds. Memoirs of the Californian Academy of Science, **8**, 1-55.

GIERLINSKI, G. 1997. Sauropod tracks in the Early Jurassic of Poland. Acta Palaeontologica Polonica, **42**, 533-538.

GILMORE, C. W. 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. Bulletin of the United States National Museum, **110**, 1-154.

— 1925. A nearly complete articulated skeleton of *Camarasaurus*, a saurischian dinosaur from the Dinosaur National Monument, Utah. Memoirs of the Carnegie Museum, **10**, 347-384.

— 1932. On a newly mounted skeleton of *Diplodocus* in the United States National Museum. Proceedings of the United States National Museum, **81**, 1-21.

— 1936. Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. Memoirs of the Carnegie Museum, **11**, 175-271.

GOLONKA, J. 2007. Late Triassic and Early Jurassic palaeogeography of the world. Palaeogeography, Palaeoclimatology, Palaeoecology, **244**, 297-307.

GOWER, D. J. and WEBER, E. 1998. The braincase of *Euparkeria*, and the evolutionary relationships of birds and crocodilians. Biological Reviews, **73**, 367-411.

— and WILKINSON, M. 1996. Is there any consensus on basal archosaur phylogeny? Proceedings of the Royal Society of London, B, **263**, 1399-1406.

GRAY, J. 1944. Studies in the mechanics of the tetrapod skeleton. Journal of Experimental Zoology, **20**, 88-116.

GREGORY, W. K. 1912. Notes on principles of quadrupedal locomotion and the mechanisms of the limbs in hoofed mammals. Annals of the New York Academy of Science, **22**, 267-294.

— and CAMP, C. L. 1918. Studies in comparative myology and osteology. No. III. Bulletin of the American Museum of Natural History, **38**, 447-563.

GRILLNER, S. 1975. Locomotion in vertebrates: central mechanisms and reflex interaction. Physiological Reviews, **55**, 247-304.

HAINES, R. W. 1935. A consideration of the constancy of muscular nerve supply. Journal of Anatomy, **70**, 33-55.

— 1939. A revision of the extensor muscles of the forearm in tetrapods. Journal of Anatomy, **73**, 211-233.

— 1946. A revision of the movements of the forearm in tetrapods. Journal of Anatomy, **80**, 1-11.

— 1950. The flexor muscles of the forearm and hand in lizards and mammals. Journal of Anatomy, **84**, 12-29.

— 1952. The shoulder joint of lizards and the primitive reptilian shoulder mechanism. Journal of Anatomy, **86**, 412-422.

— 1969. Epiphyses and sesamoids. 81-115. In GANS, C., BELLAIRS, A. D. A. and PARSONS, T. S. (eds). The Biology of the Reptilia, vol. 1, Morphology A. Academic Press, New York.

HARRIS, J. D. 2004. Confusing dinosaurs with mammals: tetrapod phylogenetics and anatomical terminology in the world of homology. The Anatomical Record Part A – Discoveries in Molecular, Cellular, and Evolutionary Biology, **281A** (2), 1240-1246.

HATCHER, J. B. 1901. *Diplodocus* (Marsh): its osteology, taxonomy, and probable habits, with a restoration of the skeleton. Memoirs of the Carnegie Museum, **1**, 1-63.

— 1902. Structure of the fore limb and manus of *Brontosaurus*. Annals of the Carnegie Museum, **1**, 356-376.

— 1903. Additional remarks on *Diplodocus*. Memoirs of the Carnegie Museum, **2**, 72-75.

HAUGHTON, S. 1866. On the muscular anatomy of the crocodile. Proceedings of the Royal Irish Academy Dublin, **9**, 268-277.

HAY, O. P. 1908. On the habits and the pose of the sauropodous dinosaurs, especially of *Diplodocus*. American Naturalist, **42**, 672-681.

— 1910. On the manner of locomotion of the dinosaurs especially *Diplodocus*, with remarks on the origin of birds. Proceedings of the Washington Academy of Science, **12**, 1-25.

— 1911. Further observations on the pose of the sauropodous dinosaurs. American Naturalist, **45**, 398-412.

HE, X. 1984. [The vertebrate fossils of Sichuan]. Sichuan Scientific and Technical Publishing House, Chengdu, Sichuan, 168 pp.

—, LI, K., CAI, K. and GAO, Y. 1984. [*Omeisaurus tianfuensis* - a new species of Omeisaurus from Dashanpu, Zigong, Sichuan]. Journal of Chengdu College of Geology, **Supplement 2**, 13-32.

—, — and — 1988. [The Middle Jurassic Dinosaur Fauna from Dashanpu, Zigong, Sichuan: Sauropod Dinosaurs. Vol. 2, *Omeisaurus tianfuensis*]. Sichuan Publishing House of Science and Technology, Chengdu, 143 pp.

—, YANG, S.-H., CAI, K.-J., LI, K. and Z.-W., L. 1996. [A new species of sauropod, *Mamenchisaurus anyuensis* sp. nov.]. Proceedings of the 30th International Geological Congress, **12**, 83-86.

—, WANG, C.-S., LIU, S.-Z., ZHOU, F.-Y., LIU, T.-Q., CAI, K.-J. and DAI, B. 1998. [A new species of sauropod dinosaur from the Early Jurassic of Gongxian County, Sichuan]. Acta Geologica Sichuan, **18** (1), 1-6.

HEDGES, S. B. and POLING, L. L. 1999. A molecular phylogeny of reptiles. Science, **283**, 998-1001.

van HEERDEN, J. 1978. *Herrerasaurus* and the origin of sauropod dinosaurs. South African Journal of Science, **74**, 187-189.

— 1979. The morphology and taxonomy of *Euskelosaurus* (Reptilia: Saurischia: Late Triassic) from South Africa. Navorsinge van die Nasionale Museum Bloemfontein, **4**, 21-84.

— 1997. Prosauropods. 242-263. In FARLOW, J. O. and BRETT-SURMAN, M. K. (eds). The Complete Dinosaur. Indiana University Press, Bloomington.

— and GALTON, P. M. 1997. The affinities of *Melanorosaurus*, a Late Triassic prosauropod dinosaur from South Africa. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **1997**, 39-55.

HILDEBRAND, M. and GOSLOW, G. E. 2001. Analysis of vertebrate structure. John Wiley and Sons Inc., New York, 373 pp.

HINIC, S. 2002. The cranial anatomy of *Massospondylus carinatus* Owen 1854 and its implications for prosauropod phylogeny. Journal of Vertebrate Paleontology, **22** (supplement to No. 3), 65A.

HOHNKE, L. A. 1973. Haemodynamics in the sauropods. Nature, **244**, 309-310.

HOLLAND, W. J. 1910. A review of some recent criticisms of the restorations of sauropod dinosaurs existing in the museums of the United States, with special reference to that of *Diplodocus carnegiei* in the Carnegie Museum. American Naturalist, **44**, 259-283.

HOLLIDAY, C. M. and WITMER, L. M. 2007. Archosaur adductor chamber evolution: integration of musculoskeletal and topological criteria in jaw muscle homology. Journal of Morphology, **268**, 457-484.

—, RIDGELY, R. C., SEDLMAYR, J. C. and WITMER, L. M. 2002. The articular cartilage of extant archosaur limb bones: implications for dinosaur functional morphology and allometry. American Zoologist, **41** (6), 1473-1474.

HOLMES, R. 1977. The osteology and musculature of the pectoral limb of small captorhinids. Journal of Morphology, **152**, 101-140.

HOLTZ, T. R. 1995a. Adaptive trends in major subgroups of theropods and related taxa. Journal of Vertebrate Paleontology, **15** (3 suppl.), 35A.

— 1995b. A new phylogeny of the Theropoda. Journal of Vertebrate Paleontology, **15** (Supplement to No. 3), 35A.

—, MOLNAR, R. E. and CURRIE, P. J. 2004. Basal Tetanurae. 71-110. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). The Dinosauria, 2nd edition. University of California Press, Berkeley.

HOTTON, N. 1980. An alternative to dinosaur endothermy: The happy wanderers. 311-350. In THOMAS, R. D. K. and OLSON, E. C. (eds). A Cold Look at the Warm-Blooded Dinosaurs. Westview Press, Boulder.

HOWELL, A. B. 1936a. Morphogenesis of the shoulder architecture. Part IV: Reptilia. Quarterly Review of Biology, **11** (2), 183-208.

— 1936b. Phylogeny of the distal musculature of the pectoral appendage. Journal of Morphology, **60**, 287-315.

— 1937. Morphogenesis of the shoulder architecture: Aves. Auk, **54**, 363-375.

HOYTE, D. A. N. and ENLOW, D. H. 1966. Wolff's law and the problem of muscle attachment on resorptive surfaces of bone. American Journal of Physical Anthropology, **24**, 205-214.

HUDSON, G. E. and LANZILLOTI, P. J. 1955. Gross anatomy of the wing muscles in the family Corvidae. American Midland Naturalist, **53**, 1-44.

— and — 1964. Muscles of the pectoral limb in galliform birds. American Midland Naturalist, **71**, 1-113.

—, SCHREIWEIS, D. O., CHEN WANG, S. Y. and LANCASTER, D. A. 1972. A numerical study of the wing and leg muscles of tinamous (Tinamidae). Northwest Science, **46**, 207-255.

von HUENE, F. 1905. Über die Trias-Dinosaurier Europas. Protokoll der Monatsberichte der Deutschen Geologischen Gesellschaft, **57**, 345-349.

— 1906. Über die Dinosaurier der aussereuropäischen Trias. Abhandlungen zur Geologie und Palaeontologie, **8**, 97-156.

— 1908. Die Dinosaurier der Europäischen Triasformation mit Berücksichtigung der außereuropäischen Vorkommnisse. Abhandlungen zur Geologie und Palaeontologie, **Supplement 1**, 1-419.

— 1909. Skizze zu einer Systematik und Stammesgeschichte der Dinosaurier. Centralblatt für Mineralogie, Geologie, und Paläontologie, **1909**, 12-22.

— 1914a. Das natürliche System der Saurischia. Centralblatt für Mineralogie, Geologie, und Paläontologie, **1914**, 156.

— 1914b. Nachträge zu meinen früheren Beschreibungen triassischer Saurischia. Geologische und Paläontologische Abhandlungen, **13**, 69-82.

— 1921. Neue Pseudosuchier und Coelurosaurier aus dem württembergischen Keuper. Acta Zoologica, **2**, 329-403.

— 1926. Vollständige Osteologie eines Plateosauriden aus dem Schwäbischen Keuper. Abhandlungen zur Geologie und Palaeontologie, **15** (2), 1-43.

— 1929. Kurze Übersicht über die Saurischia und ihre natürlichen Zusammenhänge. Paläontologische Zeitschrift, **11**, 269-273.

— 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. Monographien zur Geologie und Palaeontologie (Serie 1), **4**, 1-361.

— 1934. Ein neuer Coelurosaurier aus der thüringischen Trias. Palaeontologische Zeitschrift, **16**, 145-168.

HULKE, J. W. 1874. Note on a very large saurian limb-bone adapted for progression upon land, from the Kimmeridge Clay of Weymouth, Dorset. Quarterly Journal of the Geological Society, **30**, 16-17.

HUTCHINSON, J. R. 2001a. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). Zoological Journal of the Linnean Society, **131**, 123-168.

— 2001b. The evolution of femoral osteology and soft tissues on the line to extant birds

(Neornithes). Zoological Journal of the Linnean Society, **131**, 169-197.

— 2002. The evolution of hindlimb tendons and muscles on the line to crown-group birds. Comparative Biochemistry and Physiology Part A, **133**, 1051-1086.

— 2004. Biomechanical modeling and sensitivity analysis of bipedal running ability. II. Extinct taxa. Journal of Morphology, **262** (1), 441-461.

— 2006. The evolution of locomotion in archosaurs. Comptes Rendus Palevol, **5** (3-4), 519-530.

— and GATESY, S. M. 2000. Adductors, abductors, and the evolution of archosaur locomotion. Paleobiology, **26** (4), 734-751.

—, ANDERSON, F. C., BLEMKER, S. S. and DELP, S. L. 2005. Analysis of hindlimb muscle moment arms in *Tyrannosaurus rex* using a three-dimensional musculoskeletal computer model: implications for stance, gait, and speed. Paleobiology, **31** (4), 676-701.

HUXLEY, T. H. 1869. Further evidence of the affinity between the dinosaurian reptiles and birds. Quarterly Journal of the Geological Society, **26**, 12-31.

INTERNATIONAL COMMITTEE ON VETERINARY ANATOMICAL NOMENCLATURE, 1994. Nomina Anatomica Veterinaria, 4th edition, Nomina Histologica, reviewed 2nd edition, and Nomina Embryologica Veterinaria. International Committees on Veterinary Gross Anatomical Nomenclature, Veterinary Histological Nomenclature, and Veterinary Embryological Nomenclature, Zürich, 216 pp.

IWABE, N., HARA, Y., KUMAZAWA, Y., SHIBAMOTO, K., SAITO, Y., MIYATA, T. and KATOH, K. 2005. Sister group relationships of turtles to the bird-crocodilian clade revealed by nuclear DNA-coded proteins. Molecular Biology and Evolution, **22** (4), 810-813.

JAIN, S. L. 1973. New specimens of Lower Jurassic holostean fishes from India. Palaeontology, **16** (1), 149-177.

— 1996. Aspects of vertebrate fossils from Pranhita-Godavari Valley with emphasis on dinosaur discoveries. Journal of the Palaeontological Society of India, **41**, 1-16.

—, KUTTY, T. S., ROY-CHOWDHURY, T. and CHATTERJEE, S. 1975. The sauropod dinosaur from the Lower Jurassic Kota Formation of India. Proceedings of the Royal Society London, A, **188**, 221-228.

—, —, — and — 1979. Some characteristics of *Barapasaurus tagorei*, a sauropod dinosaur from the Lower Jurassic of Deccan, India. 204-216. In LASKAR, B. and RAJA RAO, C. S. (eds). IV International Gondwana Symposium. Vol. 1. Hindustan Publishing Corporation, Delhi.

JANENSCH, W. 1922. Das Handskelett von *Gigantosaurus robustus* und *Brachiosaurus brancai* aus den Tendaguru-Schichten Deutsch-Ostafrikas. Centralblatt für Mineralogie, Geologie und Paläontologie, **1922**, 464-480.

— 1937. Skelettrekonstruktion von *Brachiosaurus brancai* aus den Tendaguru-Schichten Deutsch-Ostafrikas. Zeitschrift der Deutschen Geologischen Gesellschaft, **89**, 550-552.

— 1961. Die Gliedmaßen und Gliedmaßengürtel der Sauropoden der Tendaguru-Schichten. Palaeontographica, **Supplement 7** (3), 177-235.

JANIS, C. M. and CARRANO, M. T. 1992. Scaling of reproductive turnover in archosaurs and mammals: why are large terrestrial mammals so rare? Annales Zoologica Fennici, **28**, 201-216.

JASINOSKI, S. C., RUSSELL, A. P. and CURRIE, P. J. 2006. An integrative phylogenetic and extrapolatory approach to the reconstruction of dromaeosaur (Theropoda: Eumaniraptora) shoulder musculature. Zoological Journal of the Linnean Society, **146** (3), 301-344.

JENKINS, F. A. 1971. The postcranial skeleton of African cynodonts. Bulletin of the Peabody Museum of Natural History, **36**, 1-216.

— 1993. The evolution of the avian shoulder joint. American Journal of Science, **293A**, 253-267.

JOHNSON, R. E. and OSTROM, J. H. 1995. The forelimb of *Torosaurus* and an analysis of the posture and gait of ceratopsian dinosaurs. 205-218. In THOMASON, J. J. (eds). Functional Morphology in Vertebrate Paleontology. Cambridge University Press, Cambridge.

JONES, S. J. and BOYDE, A. 1974. The organization and gross mineralization patterns of the collagen fibres in Sharpey fibre bone. Cell and Tissue Research, **148**, 83-96.

JUUL, L. 1994. The phylogeny of basal archosaurs. Palaeontologia Africana, **31**, 1-38.

KERMACK, D. 1984. New prosauropod material from South Wales. Zoological Journal of the Linnean Society, **82**, 101-117.

KITCHING, J. W. and RAATH, M. A. 1984. Fossils from the Elliott and Clarens Formations (Karoo sequence) of the northeastern Cape, Orange Free State and Lesotho and a suggested biozonation based on tetrapods. Palaeontologia Africana, **25**, 111-125.

KUMAZAWA, Y. and NISHIDA, M. 1999. Complete mitochondrial DNA sequences of the green turtle and blue-tailed mole skink: statistical evidence for archosaurian affinity of turtles. Molecular Biology and Evolution, **16**, 784-792.

LANDSMEER, J. M. F. 1983. The Mechanism of Forearm Rotation in *Varanus exanthematicus*. Journal of Morphology, **175**, 119-130.

— 1984. Morphology of the anterior limb in relation to sprawling gait in *Varanus*. Symposium of the Zoological Society London, **52**, 27-45.

LANGER, M. C. 2003. The pelvic and hind limb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Late Triassic, Brazil). PaleoBios, **23** (2), 1-40.

— 2004. Basal Saurischia. 25-46. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). The Dinosauria, second edition. University of California Press, Berkeley.

— and BENTON, M. J. 2006. Early dinosaurs: a phylogenetic study. Journal of Systematic Palaeontology, **4**, 309-358.

— , ABDALA, F., RICHTER, M. and BENTON, M. J. 1999. A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. Comptes Rendus de l' Academie de Sciences Serie IIa: Sciences de la Terre et des Planetes, **329** (7), 511-517.

—, FRANÇA, M. A. G. and GABRIEL, S. 2007. The pectoral girdle and forelimb anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Upper Triassic, Brazil). Special Papers in Palaeontology, **77**, 113-137.

LANYON, L. E. 1980. The influence of function on the development of bone curvature. An experimental study on the rat tibia. Journal of Zoology London, **192**, 457-466.

— 1981. Locomotor loading and functional adaptation in limb bones. Symposia of the Zoological Society of London, **48**, 305-329.

LARSON, P. L. and RIGBY, J. K., JR. 2005. Furcula of *Tyrannosaurus rex*. 247-255. In CARPENTER, K. (eds). The Carnivorous Dinosaurs. Indiana University Press, Bloomington.

LAVAS, J. R. 1997. Asian Dinosaur Hunters. In J. O. Farlow and M. K. Brett-Surman (eds). The complete dinosaur. Indiana University Press, Bloomington, 34-42 pp.

LEAL, L. A., AZEVEDO, S. A. K. D., KELLNER, A. W. A. and ROSA, A. A. S. 2004. A new early dinosaur (Sauropodomorpha) from the Caturrita Formation (Late Triassic), Paraná Basin, Brazil. Zootaxa, **690**, 1-24.

LEIDY, J. 1865. Memoir of the extinct reptiles of the Cretaceous formations of the United States. Smithsonian Contributions to Knowledge, **14**, 1-135.

LIEM, K. F., BEMIS, W. E., WALKER, W. F. and GRANDE, L. 2001. Functional anatomy of the vertebrates. Harcourt College Publishers, New York, 703 pp.

LÜ, J., LI, S., JI, Q., WANG, G., ZHANG, J. and DONG, Z. 2006. New eusauropod dinosaur from Yuanmou of Yunnan Province, China. Acta Geologica Sinica - English Edition, **80** (1), 1-10.

—, LI, T., ZHONG, S., AZUMA, Y., FUJITA, M., DONG, Z. and JI, Q. 2007. New yunnanosaurid dinosaur (Dinosauria, Prosauropoda) from the Middle Jurassic Zhanghe Formation of Yuanmou, Yunnan Province of China. Memoir of the Fukui Prefectural Dinosaur Museum, **6**, 1-15.

LULL, R. S. 1905. Restoration of the horned dinosaur *Diceratops*. American Journal of Science, Series 3, **20**, 420-422.

— 1910. *Stegosaurus ungulatus* Marsh, recently mounted at the Peabody Museum of Yale University. American Journal of Science, Series 4, **30**, 361-376.

— 1953. Triassic Life of the Connecticut Valley. Revised edition. Connecticut State Geology and Natural History Survey Bulletin, **81**, 1-336.

LUO, Y. N. and WANG, C. S. 1999. New discovery on dinosaur fossils from Early Jurassic, Sichuan, China. Chinese Science Bulletin, **44** (23), 2182-2188.

— and — 2000. A new sauropod, *Gongxianosaurus*, from the lower Jurassic of Sichuan, China. Acta Geologica Sinica - English Edition, **74** (2), 132-136.

—, — and YOU, H. L. 1999. A basal sauropomorph from the Early Jurassic of Sichuan Basin, south China. Journal of Vertebrate Paleontology, **19** (supplement to No. 3), 60A.

LUO, Z. and WU, X. C. 1994. The small tetrapods of the Lower Lufeng Formation, Yunnan, China. 251-270. In FRASER, N. C. and SUES, H. D. (eds). In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press, Cambridge.

MACALISTER, A. 1864. On the anatomy of the ostrich (*Struthio camelus*). Proceedings of the Royal Irish Academy, **9**, 1-24.

MACCONNAILL, M. A. 1950. The movements of bones and joints: The synovial fluid and its assistants. Journal of Bone and Joint Surgery, **32B**, 244-252.

MAIER, G. 2003. African Dinosaurs Unearthed: The Tendaguru Expeditions. Indiana University Press, Bloomington 512 pp.

MAKOVICKY, P. J. and CURRIE, P. J. 1998. The presence of a furcula in tyrannosaurid theropods, and its phylogenetic and functional implications. Journal of Vertebrate Paleontology, **18**, 143-149.

MARSH, O. C. 1877a. Notice of a new and gigantic dinosaur. American Journal of Science, Series 3, **14**, 87-88.

— 1877b. Notice of some new dinosaurian reptiles from the Jurassic Formation. American Journal of Science, Series 3, **14**, 514-516.

— 1878. Notice of new dinosaurian reptiles. American Journal of Science, Series 3, **15**, 241-244.

— 1883. Principal characters of American Jurassic dinosaurs. Part VI: Restoration of Brontosaurus. American Journal of Science, Series 3, **26**, 81-85.

— 1884a. Principal characters of American Jurassic dinosaurs. Part VII. On the Diplodocidae, a new family of the Sauropoda. American Journal of Science, Series 3, **27**, 161-167.

— 1884b. Principal characters of American Jurassic dinosaurs. Part VIII. The order

Theropoda. American Journal of Science, Series 3, **27**, 329-340.

— 1891. Restoration of *Stegosaurus*. American Journal of Science, Series 3, **42**, 179-181.

— 1892. Restorations of *Claosaurus* and *Ceratosaurus*. American Journal of Science, Series 3, **44**, 343-349.

MARTÍNEZ, R. N. 2002. The monophyly and interrelationships of Prosauropoda. Journal of Vertebrate Paleontology, **22** (supplement to No. 3), 84A.

MATSUDA, Y., NISHIDA-UMEHARA, C., TARUI, H., KUROIWA, A., YAMADA, K., ISOBE, T., ANDO, J., FUJIWARA, A., HIRAO, Y., NISHIMURA, O., ISHIJIMA, J., HAYASHI, A., SAITO, T., MURAKAMI, T., MURAKAMI, Y., KURATANI, S. and AGATA, K. 2005. Highly conserved linkage homology between birds and turtles: Bird and turtle chromosomes are precise counterparts of each other. Chromosome Research, **13** (6), 601-615.

MATTHEW, W. D. 1910. The pose of sauropodous dinosaurs. American Naturalist, **44**, 547-560.

MAUERSBERGER, M. 2005. Morphometrische Untersuchungen der Vorder- und Hinterextremitäten der basalen Sauropodomorpha. Unpublished diploma thesis. Freie Universität Berlin, Berlin, 48 pp.

MAZIN, J. M., HANTZPERGUE, P., LAFAURIE, G. and VIGNAUD, P. 1995. Pterosaur Trackways from the Tithonian of Crayssac (Quercy, France). Comptes Rendus de l'Academie des Sciences, Serie II Fascicule A, Sciences de la Terre et des Planetes, **321**, 417-424.

MAZZETTA, G. V., CHRISTIANSEN, P. and FARINA, R. A. 2004. Giants and bizarres: Body size of some southern South American Cretaceous dinosaurs. Historical Biology, **2004**, 1-13.

MCCUTCHEN, C. W. 1983. Lubrication of and by cartilage. In B. K. Hall (ed). Cartilage, vol. 2. Academic Press, New York, 87-107 pp.

MCGOWAN, C. 1979. The hind limb musculature of the brown Kiwi, *Apteryx australis mantelli*. Journal of Morphology, **160** (1), 33-74.

— 1982. The wing musculature of the brown kiwi, *Apteryx australis mantelli* and its bearing on ratite affinities. Journal of Zoology London, **197**, 173-219.

— 1986. The wing musculature of the Weka (*Gallirallus australis*), a flightless rail endemic to New Zealand. Journal of Zoology London A, **210**, 305-346.

MCINTOSH, J. S. 1990a. Sauropoda. 345-401. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). The Dinosauria. University of California Press, Berkeley.

— 1990b. Species determination in sauropod dinosaurs with tentative suggestions for their classification. 53-69. In CARPENTER, K. and CURRIE, P. J. (eds). Dinosaur systematics. Approaches and perspectives. Cambridge University Press, Cambridge.

— 1997. Sauropoda. 654-658. In CURRIE, P. J. and PADIAN, K. (eds). Encyclopedia of Dinosaurs. Academic Press, San Diego.

MECKEL, J. F. 1828. System der vegleichenden Anatomie, Dritter Theil. Rengersche Buchhandlung, Halle, 267 pp.

MEERS, M. B. 2003. Crocodylian Forelimb Musculature and Its Relevance to Archosauria. The Anatomical Record Part A – Discoveries in Molecular, Cellular, and Evolutionary Biology, **274A**, 891-916.

MINER, R. W. 1925. The pectoral limb of *Eryops* and other primitive tetrapods. Bulletin of the American Museum of Natural History, **51**, 145-312.

MIVART, G. 1867. Notes on the myology of *Iguana tuberculata*. Proceedings of the Zoological Society London, **1867**, 766-797.

— 1870. On the myology of *Chamaeleon parsonii*. Proceedings of the Zoological Society

London, **1870**, 850-890.

MONBARON, M., RUSSELL, D. A. and TAQUET, P. 1999. *Atlasaurus imelakei* n.g., n.sp., a brachiosaurid-like sauropod from the Middle Jurassic of Morocco. Comptes Rendus de l' Academie de Sciences Serie IIa: Sciences de la Terre et des Planetes, **329** (7), 519-526.

MYERS, E. R. 1983. Biomechanics of cartilage and its response to biomechanical stimuli. In B. K. Hall (ed). Cartilage, vol. 1. Academic Press, New York, 313-341 pp.

NICHOLLS, E. L. and RUSSELL, A. P. 1985. Structure and function of the pectoral girdle and forelimb of *Struthiomimus altus* (Theropoda: Ornithomimidae). Palaeontology, **28**, 643-677.

NORMAN, D. B., SUES, H. D., WITMER, L. M. and CORIA, R. A. 2004. Basal Ornithopoda. In D. B. Weishampel, et al. (eds). The Dinosauria, 2nd edition. University of California Press, Berkeley, 393-412 pp.

NOVAS, F. E. 1992. Phylogenetic relationships of the basal dinosaurs, the Herrerasauridae. Palaeontology, **35** (1), 51-62.

— 1993. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. Journal of Vertebrate Paleontology, **13**, 400-423.

— 1996. Dinosaur monophyly. Journal of Vertebrate Paleontology, **16** (4): 723-741.

— 1997. Herrerasauridae. 303-311. In CURRIE, P. J. and PADIAN, K. (eds). Encyclopedia of Dinosaurs. Academic Press, San Diego.

OLSEN, P. E. and GALTON, P. M. 1984. A review of the reptile and amphibian assemblages from the Stormberg Group of southern Africa with special emphasis on the footprints and the age of the Stormberg. Palaeontologia Africana, **25**, 87-110.

OSBORN, H. F. 1904. On the position of the bones of the forearm in the Opisthocoelia or Sauropoda. Science, **19**, 255-256.

— and GRANGER, W. 1901. Fore and hind limbs of Sauropoda from the Bone Cabin quarry. Bulletin of the American Museum of Natural History, **24**, 199-208.

OSTROM, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. Bulletin of the Peabody Museum of Natural History (Yale University), **30**, 1-165.

— 1974. The pectoral girdle and forelimb function of *Deinonychus* (Reptilia: Saurischia): A correction. Postilla, Yale Peabody Museum, **165**, 1-11.

— 1976. Some hypothetical anatomical stages in the evolution of avian flight. Smithsonian Contributions to Paleobiology, **27**, 1-27.

PADIAN, K. 1997a. Bipedality. 68-70. In CURRIE, P. J. and PADIAN, K. (eds). Encyclopedia of Dinosaurs. Academic Press, San Diego.

— 1997b. Saurischia. 647-653. In CURRIE, P. J. and PADIAN, K. (eds). Encyclopedia of Dinosaurs. Academic Press, San Diego.

— 1997c. Pectoral Girdle. 530-536. In CURRIE, P. J. and PADIAN, K. (eds). Encyclopedia of Dinosaurs. Academic Press, San Diego.

PARRISH, J. M. 1997. Archosauria. 20-24. In CURRIE, P. J. and PADIAN, K. (eds). Encyclopedia of Dinosaurs. Academic Press, San Diego.

— and STEVENS, K. A. 2002. Rib angulation, scapular position, and body profiles in sauropod dinosaurs. Journal of Vertebrate Paleontology, **22** (supplement to No. 3), 95A.

PARSONS, F. G. 1905. On pressure epiphyses. Journal of Anatomy and Physiology, **39**, 402-412.

PAUL, G. S. 1998. Terramegathermy and Cope's Rule in the land of titans. Modern Geology, **23**, 179-217.

PENG, G., YE, Y., GAO, Y., SHU, C. and JIANG, S. 2005. Jurassic Dinosaur Faunas in Zigong. Sichuan People's Publishing House, Zigong, 236 pp.

PERRY, F. S. and REUTER, T. 1999. Hypothetical lung structure of *Brachiosaurus* based on functional constraints. Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe, **2**, 75-79.

PI, L.-H., OUYANG, H. and YE, Y. 1996. [A new species of sauropod from Zigong, Sichuan: *Mamenchisaurus youngi*]. 87-91. In Department of Spatial Planning and Regional Economy (eds). [Papers on Geoscience Contributed to the 30th International Geological Congress]. China Economic Publishing House, Beijing.

—, — and — 2002. The first mamenchisaurian skeleton with complete skull, *Mamenchisaurus youngi*. Zigong Dinosaur Museum, Zigong, 111 pp.

PISANI, D., YATES, A. M., LANGER, M. C. and BENTON, M. J. 2002. A genus-level supertree of the dinosauria. Proceedings of the Royal Society of London Biological Sciences, **269** (1494), 915-921.

POL, D. and POWELL, J. E. 2007. New information on *Lessemsaurus sauropoides* (Dinosauria: Sauropodomorpha) from the Upper Triassic of Argentina. Special Papers in Palaeontology, **77**, 223-243.

RAATH, M. A. 1972. Fossil vertebrate studies in Rhodesia: a new dinosaur (Reptilia: Saurischia) from near the Triassic-Jurassic boundary. Arnoldia, **5** (30), 1-37.

— 1977. The anatomy of the Triassic theropod *Syntarsus rhodesiensis* (Saurischia: Podokesauridae) and a consideration of its biology. PhD dissertation, Rhodes University, Grahamstown, South Africa.

RABL, C. 1916. Über die Muskeln und Nerven der Extremitäten von *Iguana tuberculata* Gray. Anatomische Hefte, **53**, 681-789.

RAIKOW, R. J., BLEDSOE, A. H., MYERS, B. A. and WELSH, C. J. 1990. Individual variation in avian muscles and its significance for the reconstruction of phylogeny. Systematic Zoology, **39**, 362-370.

RAUHUT, O. W. M. 2003a. The interrelationships and evolution of basal theropod dinosaurs. Special Papers in Palaeontology, **69**, 1-213.

— 2003b. A dentary of *Patagosaurus* (Sauropoda) from the Middle Jurassic of Patagonia. Ameghiniana, **40**, 425-432.

— et al. in preparation. Saurischia. In SUES, H.-D. (ed.): Handbook of Paleoherpetology, Part 14, second edition. Verlag Dr. Friedrich Pfeil, München.

—, REMES, K., FECHNER, R., CLADERA, G. and PUERTA, P. 2005. Discovery of a short-necked sauropod dinosaur from the Late Jurassic of Patagonia. Nature, **435** (7042), 670-672.

REIG, O. A. 1963. La presencia de dinosaurios saurisquios en los 'Estrados de Ischigualasto' (Mesotriásico superior) de las Provincias de San Juan y La Rioja (Republica Argentina). Ameghiniana, **3**, 3-20.

REISZ, R. R., SCOTT, D., SUES, H. D., EVANS, D. C. and RAATH, M. A. 2005. Embryos of an Early Jurassic prosauropod dinosaur and their evolutionary significance. Science, **309** (5735), 761-764.

REST, J. S., AST, J. C., AUSTIN, C. C., WADDELL, P. J., TIBBETTS, E. A., HAY, J. M. and MINDELL, D. P. 2003. Molecular systematics of primary reptilian lineages and the tuatara mitochondrial genome. Molecular Phylogenetics and Evolution, **29**, 289-297.

RIBBING, L. 1907. Die distale Armmuskulatur der Amphibien, Reptilien und Säugetiere. Zoologisches Jahrbuch, Abteilung Anatomie und Ontogenie der Tiere, **23**, 587-682.

— 1938. Die Muskeln und Nerven der Extremitäten. 543-656. In BOLK, L. (ed). Handbuch der vergleichenden Anatomie der Wirbeltiere, Band V. Urban und Schwarzenberg, Berlin.

RIEPPEL, O. 1999. Einführung in die computergestützte Kladistik. Verlag Dr. Friedrich Pfeil, München, 112 pp.

RIGGS, E. S. 1901. The fore leg and pectoral girdle of *Morosaurus*; with a note on the genus *Camarosaurus*. Publications of the Field Columbian Museum, Geology Series, **1** (10), 275-281.

— 1904. Structure and relationships of opisthocoelian dinosaurs. Part II. The Brachiosauridae. Field Columbian Museum Publications, Geological Series, **2**, 229-247.

RINEHART, L. F., LUCAS, S. G. and HUNT, A. P. 2007. Furculae in the Late Triassic theropod dinosaur *Coelophysis bauri*. Paläontologische Zeitschrift, **81**, 174-180.

ROGERS, R. R., ARCUCCI, A. B., ABDALA, F., SERENO, P. C., FORSTER, C. A. and MAY, C. L. 2001. Paleoenvironment and taphonomy of the Chañares Formation tetrapod assemblage (Middle Triassic), northwestern Argentina: Spectacular preservation in volcanogenic concretions. Palaios, **16**, 461-481.

ROMER, A. S. 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. Bulletin of the American Museum of Natural History, **46**, 517-606.

— 1923. The pelvic musculature of saurischian dinosaurs. Bulletin of the American Museum of Natural History, **58** (19), 605-617.

— 1924. Pectoral limb musculature and shoulder-girdle structure in fish and tetrapods. Anatomical Record, **27**, 119-143.

— 1942. The development of tetrapod limb musculature - the thigh of *Lacerta*. Journal of Morphology, **71**, 251-298.

— 1944. The development of tetrapod limb musculature - the shoulder region of *Lacerta*. Bulletin of the American Museum of Natural History, **74**, 1-41.

— 1956. Osteology of the Reptiles. University of Chicago Press, Chicago, 772 pp.

— 1966. Vertebrate Paleontology, third edition. University of Chicago Press, Chicago, 468 pp.

— 1971. The Chañares (Argentina) Triassic reptile fauna. X. Two new but incompletely known long-limbed pseudosuchians. Breviora, **394**: 107.

— 1972a. The Chañares (Argentina) Triassic reptile fauna. XV. Further remains of the thecodonts *Lagerpeton* and *Lagosuchus*. Breviora, **394**: 1-7.

— 1972b. The Chañares (Argentina) Triassic reptile fauna. XIV. *Lewisuchus admixtus* gen. et sp. nov., a further thecodont from the Chañares beds. Breviora, **390**, 1-13.

ROWE, T. 1989. A new species of the theropod dinosaur *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. Journal of Vertebrate Paleontology, **9**, 125-136.

— and GAUTHIER, J. A. 1990. Ceratosauria. 151-168. In WEISHAMPEL, D. B., DODSON, P. and OSMOLSKA, H. (eds). The Dinosauria. University of California Press, Berkeley.

RÜHLE VON LILIENSTERN, J., LANG, M. and HUENE, F. V. 1952. Die Saurier Thüringens. Gustav Fischer, Jena, 40 pp.

RUSSELL, L. S. 1935. Musculature and function in the Ceratopsia. Bulletin of the National Museum of Canada, **77**, 39-48.

SALGADO, L., CORIA, R. A. and CALVO, J. O. 1997. Evolution of titanosaurid sauropods. I: phylogenetic analysis based on the postcranial evidence. Ameghiniana, **34** (1), 3-32.

SANDER, P. M. 1999. Life history of Tendaguru sauropods as inferred from long bone histology. Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe, **2**, 103-112.

— 2000. Long bone histology of the Tendaguru sauropods: Implications for growth and biology. Paleobiology, **26** (3), 466-488.

— and KLEIN, N. 2005. Developmental plasticity in the life history of a prosauropod dinosaur. Science, **310** (5755), 1800-1802.

—, —, BUFFETAUT, E., CUNY, G., SUTEETHORN, V. and LE LOEUFF, J. 2004. Adaptive radiation in sauropod dinosaurs: bone histology indicates rapid evolution of giant body size through acceleration. Organisms Diversity and Evolution, **4** (3), 165-173.

—, MATEUS, O., LAVEN, T. and KNÖTSCHKE, N. 2006. Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur. Nature, **441** (7094), 739-741.

SANDERS, A. 1870. Notes on the myology of *Platydactylus japonicus*. Proceedings of the Zoological Society London, **1870**, 413-426.

— 1872. Notes on the myology of *Liolepis belli*. Proceedings of the Zoological Society London, **1872**, 154-183.

— 1874. Notes on the myology of the *Phyrnosoma coronatum*. Proceedings of the Zoological Society London, **1874**, 71-89.

SANTA LUCA, A. P. 1980. The postcranial skeleton of *Heterodontosaurus tucki* (Reptilia, Ornithischia) from the Stormberg of South Africa. Annals of the South Africa Museum, **79**, 159-211.

dos SANTOS, V. F., LOCKLEY, M. G., MEYER, C. A., CARVALHO, J., GALOPIM DE CARVALHO, A. M. and MORATALLA, J. J. 1994. A new sauropod tracksite from the Middle Jurassic of Portugal. GAIA, **10**, 5-14.

SCHREIWEIS, D. O. 1982. A comparative study of the appendicular musculature of penguins (Aves: Sphenisciformes). Smithsonian Contributions to Zoology, **341**, 1-46.

SCHWARZ, D., FREY, E. and MEYER, C. A. 2007a. Novel reconstruction of the orientation of the pectoral girdle in sauropods. Anatomical Record, **290** (1), 32-47.

—, WINGS, O. and MEYER, C. A. 2007b. Super sizing the giants: first cartilage preservation at a sauropod dinosaur limb joint. Journal of the Geological Society, London, **164**, 61-65.

SENTER, P. 2006a. Forelimb function in *Ornitholestes hermanni* Osborn (Dinosauria, Theropoda). Palaeontology, **49** (5), 1029-1034.

— 2006b. Scapular orientation in theropods and basal birds, and the origin of flapping flight. Acta Palaeontologica Polonica, **51** (2), 305-313.

— 2007. Analysis of forelimb function in basal ceratopsians. Journal of Zoology, **273** (3), 305-314.

— and ROBINS, J. H. 2005. Range of motion in the forelimb of the theropod dinosaur *Acrocanthosaurus atokensis*, and implications for predatory behaviour. Journal of Zoology, **266**, 307-318.

SERENO, P. C. 1989. Prosauropod monophyly and basal sauropodomorph phylogeny. Journal of Vertebrate Paleontology, **9** (supplement to No. 3), 38A.

— 1991. Basal archosaurs: phylogenetic relationships and functional implications. Society of Vertebrate Paleontology Memoirs, **2**: 1-53.

— 1993. The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. Journal of Vertebrate Paleontology, **13**, 425-450.

— 1997. The origin and evolution of dinosaurs. Annual Review of Earth and Planetary Sciences, **25**, 435-489.

— 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **210**, 41-83.

— 1999a. The evolution of dinosaurs. Science, **284** (5423), 2137-2147.

— 1999b. A rationale for dinosaurian taxonomy. Journal of Vertebrate Paleontology, **19**, 788-790.

— and ARCUCCI, A. B. 1994. Dinosaur precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis* gen. nov. Journal of Vertebrate Paleontology, **14**, 53-73.

—, FORSTER, C. A., ROGERS, R. R. and MONETTA, A. M. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. Nature, **361**, 64-66.

—, BECK, A. L., DUTHEIL, D. B., LARSSON, H. C. E., LYON, G. H., MOUSSA, B., SADLEIR, R. W., SIDOR, C. A., VARRICCHIO, D. J., WILSON, G. P. and WILSON, J. A. 1999. Cretaceous sauropods from the sahara and the uneven rate of skeletal evolution among dinosaurs. Science, **286** (5443), 1342-1347.

SEYMOUR, R. S. and LILLYWHITE, H. B. 2000. Hearts, neck posture and metabolic intensity of sauropod dinosaurs. Proceedings of the Royal Society of London Biological Sciences, **267** (1455), 1883-1887.

SMITH, M. and CARPENTER, K. 1990. Forelimb biomechanics of *Tyrannosaurus rex*. Journal of Vertebrate Paleontology, **10** (Supplement 3), 43A.

STEINER, H. 1949. Zur Frage der ehemaligen Flugfähigkeit der Ratiten. Revue Suisse de Zoologie, **56**, 364-372.

STEVENS, K. A. and PARRISH, J. M. 1999. Neck posture and feeding habits of two jurassic sauropod dinosaurs. Science, **284** (5415), 798-800.

— and — 2005a. Neck posture, dentition, and feeding strategies in Jurassic sauropod dinosaurs. 212-232. In TIDWELL, V. and CARPENTER, K. (eds). Thunder-Lizards: The Sauropodomorph Dinosaurs. Indiana University Press, Bloomington.

— and — 2005b. Digital reconstructions of sauropod dinosaurs and implications for feeding. 178-200. In CURRY ROGERS, K. and WILSON, J. A. (eds). The Sauropods: Evolution and Paleobiology. University of California Press, Berkeley.

SUES, H. D. 1997. European Dinosaur Hunters. In J. O. Farlow and M. K. Brett-Surman (eds). The complete dinosaur. Indiana University Press, Bloomington, 12-23 pp.

—, OLSEN, P. E., CARTER, J. G. and SCOTT, D. M. 2003. A new crocodylomorph archosaur from the Upper Triassic of North Carolina. Journal of Vertebrate Paleontology, **23** (2), 329-343.

SULLIVAN, G. E. 1962. Anatomy and embryology of the wing musculature of the domestic fowl. Australian Journal of Zoology, **10**, 458-518.

SY, M. 1936. Funktionell-anatomische Untersuchungen am Vogelflügel. Journal of Ornithology, **84**, 199-296.

TANG, F., JIN, X.-S., KANG, X.-M. and ZHANG, G. 2001. *Omeisaurus maoianus*, a complete Sauropoda from Jingyan, Sichuan. China Ocean Press, Beijing, 128 pp.

THOMPSON, S. and HOLMES, R. 2007. Forelimb Stance and Step Cycle in *Chasmosaurus irvinenesis* (Dinosauria: Neoceratopsia). Palaeontologia Electronica, **10** (1.5A), 1-17.

THULBORN, R. A. 1982. Speeds and gaits of dinosaurs. Palaeogeography, Palaeoclimatology, Palaeoecology, **38**, 227-256.

THULBORN, T. 2006. On the tracks of the earliest dinosaurs: implications for the hypothesis of dinosaurian monophyly. Alcheringa, **30**, 273-311.

TORNIER, G. 1909. Wie war der *Diplodocus carnegii* wirklich gebaut? Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin, **1909**, 193-209.

TYKOSKI, R. and ROWE, T. 2004. Ceratosauria. In D. B. Weishampel, et al. (eds). The Dinosauria, 2nd edition. University of California Press, Berkeley, 47-70 pp.

—, FORSTER, C. A., ROWE, T., SAMPSON, S. D. and MUNYIKWA, D. 2002. A furcula in the Coelophysid theropod *Syntarsus*. Journal of Vertebrate Paleontology, **22**, 728-733.

UNWIN, D. M. 1996. Pterosaur tracks and the terrestrial ability of pterosaurs. Lethaia, **29**, 373-386.

— 1999. Pterosaurs: back to the traditional model? Trends in Ecology & Evolution, **14**, 263-268.

UPCHURCH, P. 1994. Manus claw function in sauropod dinosaurs. GAIA, **10**, 161-171.

— 1995. The evolutionary history of sauropod dinosaurs. Philosophical Transactions, Royal Society of London, B, **349** (1330), 365-390.

— 1997a. Prosauropoda. 599-607. In CURRIE, P. J. and PADIAN, K. (eds). Encyclopedia of Dinosaurs. Academic Press, San Diego.

— 1997b. Sauropodomorpha. 658-660. In CURRIE, P. J. and PADIAN, K. (eds). Encyclopedia of Dinosaurs. Academic Press, San Diego.

— 1998. The phylogenetic relationships of sauropod dinosaurs. Zoological Journal of the Linnean Society, **124**, 43-103.

— 1999. The phylogenetic relationships of the Nemegtosauridae (Saurischia, Sauropoda). Journal of Vertebrate Paleontology, **19**, 106-125.

— and BARRETT, P. M. 2000. The evolution of sauropod feeding mechanisms. 79-122. In SUES, H. D. (ed). Evolution of herbivory in terrestrial vertebrates. Cambridge University Press, Cambridge.

— and MARTIN, J. 2002. The Rutland *Cetiosaurus*: The anatomy and relationships of a Middle Jurassic British sauropod dinosaur. Palaeontology, **45** (6), 1049-1074.

— and — 2003. The anatomy and taxonomy of *Cetiosaurus* (Saurischia, Sauropoda) from the Middle Jurassic of England. Journal of Vertebrate Paleontology, **23** (1), 208-231.

—, BARRETT, P. M. and DODSON, P. 2004. Sauropoda. 259-322. In WEISHAMPEL, D. B., DODSON, P. and OSMOLSKA, H. (eds). The Dinosauria, second edition. University of California Press, Berkeley.

—, — and GALTON, P. M. 2007. A phylogenetic analysis of basal sauropodmorph relationships: implications for the origin of sauropod dinosaurs. Special Papers in Palaeontology, **77**, 57-90.

VANDEN BERGE, J. C. 1979. Myologia. 175-219. In BAUMEL, J. J., KING, A. S., LUCAS, A. M., BREAZILE, J. E. and EVANS, H. E. (eds). Nomina Anatomica Avium. Academic Press, London.

— and ZWEERS, G. A. 1993. Myologia. 189-247. In BAUMEL, J. J., KING, A. S., BREAZILE, J. E., EVANS, H. E. and VANDEN BERGE, J. C. (eds). Handbook of Avian Anatomy: Nomina Anatomica Avium. Nuttall Ornithological Club, Cambridge.

VARGAS, A. O. and FALLON, J. F. 2005a. Birds have dinosaur wings: The molecular evidence. Journal of Experimental Zoology Part B (Molecular and Developmental Evolution), 304B (1), 86-90.

— and — 2005b. The digits of the wing of birds are 1, 2, and 3. A review. Journal of Experimental Zoology Part B (Molecular Development and Evolution), 304B (3), 206-

219.

de VIS, C. W. 1884. Myology of *Chlamydosaurus kingii*. Proceedings of the Linnean Society of New South Wales, **1884**, 300-320.

VOLLMERHAUS, B., SINOWATZ, F., FREIWEIN, J. and WAIBL, H. 1992. Lehrbuch der Anatomie der Haustiere, Band V: Anatomie der Vögel. Verlag Paul Parey, Berlin, 446 pp.

WAGNER, A. 1861. Neue Beiträge zur Kenntnis der urweltlichen Fauna des lithographischen Schiefers. V. *Compsognathus longipes* Wagn. Abhandlungen der Bayerischen Akademie der Wissenschaften, **9**, 30-38.

WALKER, A. D. 1990. A revision of *Sphenosuchus acutus* Haughton, a crocodylomorph reptile from the Elliot Formation (Late Triassic or Early Jurassic) of South Africa. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, **330**, 1-120.

WALKER, W. F. 1947. The development of the shoulder region of the turtle, *Chrysemys picta marginata*, with special reference to the primary musculature. Journal of Morphology, **80** (2), 195-249.

— 1973. The locomotor apparatus of testudines. 1-100. In GANS, C. (ed). Biology of the reptilia. Vol. IV. Morphology, part D. Academic Press, New York.

WALTER, L. R. 1986. The limb posture of kannemeyeriid dicynodonts: functional and ecological considerations. 89-97. In PADIAN, K. (ed). The Beginning of the Age of Dinosaurs. Cambridge University Press, Cambridge.

WALTHALL, J. C. and ASHLEY-ROSS, M. A. 2006. Postcranial Myology of the California Newt, *Taricha torosa*. The Anatomical Record Part A, **288A**, 46-57.

WANG, Y.-G. and SUN, D.-L. 1983. A survey of the Jurassic System of China. Canadian Journal of Earth Sciences, **20**, 1646-1656.

WEAVER, J. C. 1983. The improbable endotherm: the energetics of the sauropod dinosaur *Brachiosaurus*. Paleobiology, **9**, 173-182.

WEDEL, M. J. 2003. Vertebral pneumaticity, air sacs, and the physiology of sauropod dinosaurs. Paleobiology, **29** (2), 243-255.

— 2005. Postcranial pneumaticity in sauropods and its implications for mass estimates. 201-228. In CURRY ROGERS, K. and WILSON, J. A. (eds). The Sauropods: Evolution and Paleobiology. University of California Press, Berkeley.

WEISHAMPEL, D. B. and WITMER, L. M. 1990. Heterodontosauridae. 486-497. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). The Dinosauria. University of California Press, Berkeley.

—, DODSON, P. and OSMÓLSKA, H. (eds) 2004a. The Dinosauria, second edition. University of California Press, Berkeley, 861 pp.

—, BARRETT, P. M., CORIA, R. A., LE LOEUFF, J., XU, X., ZHAO, X., SAHNI, A., GOMANI, E. M. and NOTO, C. R. 2004b. Dinosaur Distribution. 517-606. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). The Dinosauria, 2nd edition. University of California Press, Berkeley.

WELLES, S. P. 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda). Osteology and comparisons. Palaeontographica A, **185**, 85-180.

WILD, R. 1978. Ein Sauropoden-Rest (Reptilia, Saurischia) aus dem Posidonienschiefer (Lias, Toarcium) von Holzmaden. Stuttgarter Beiträge zur Naturkunde, Serie B: Geologie und Paläontologie, **41**, 1-15.

WILHITE, D. R. 2003. Biomechanical reconstruction of the appendicular skeleton in three North American jurassic sauropods. PhD Dissertation, Louisiana State University, 224 pp.

WILKINSON, M., THORLEY, J. L. and UPCHURCH, P. 2000. A chain is no stronger than its weakest link: Double decay analysis of phylogenetic hypotheses. Systematic Biology, **49**, 754-776.

WILSON, J. A. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. Journal of Vertebrate Paleontology, **19**, 639-653.

— 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zoological Journal of the Linnean Society, **136**, 217-276.

— 2005. Integrating ichnofossil and body fossil records to estimate locomotor posture and spatiotemporal distribution of early sauropod dinosaurs: a stratocladistic approach. Paleobiology, **31** (3), 400-423.

— 2006. Anatomical nomenclature of fossil vertebrates: standardized terms or 'lingua franca'? Journal of Vertebrate Paleontology, **26** (3), 511-518.

— and CARRANO, M. T. 1999. Titanosaurs and the origin of "wide-gauge" trackways: A biomechanical and systematic perspective on sauropod locomotion. Paleobiology, **25** (2), 252-267.

— and SERENO, P. C. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Society of Vertebrate Paleontology Memoir, **5**, 1-68.

WITMER, L. M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. 19-33. In THOMASON, J. J. (ed). Functional morphology in vertebrate paleontology. Cambridge University Press, Cambridge.

— 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. Journal of Vertebrate Paleontology, **17** (supplement to 1), 1-73.

WOLFF, J. 1892. Das Gesetz der Transformation der Knochen. Hirschwald, Berlin.

WOODWARD, A. S. 1907. On a new dinosaurian reptile (*Scleromochlus taylori*, gen. et sp. nov.) from the Trias of Lossiemouth, Elgin. Quarterly Journal of the Geological Society, **63**: 140-144.

YADAGIRI, P. 1988. A new sauropod *Kotasaurus yamanpalliensis* from Lower Jurassic Kota Formation of India. Journal of the Geological Survey of India, **11**, 102-127.

— 2001. The osteology of *Kotasaurus yamanpalliensis*, a sauropod dinosaur from the Early Jurassic Kota Formation of India. Journal of Vertebrate Paleontology, **21**, 242-252.

—, PRASAD, K. N. and SATSANGI, P. P. 1979. The sauropod dinosaur from the Kota Formation of Pranhitagodavari Valley, India. 199-202. In (eds). 4th International Gondwana Symposium.

YATES, A. M. 2001. A new look at *Thecodontosaurus* and the origin of sauropod dinosaurs. Journal of Vertebrate Paleontology, **21** (supplement to No. 3), 116A.

— 2003a. A new species of the primitive dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. Journal of Systematic Palaeontology, **1** (1), 1-42.

— 2003b. The species taxonomy of the sauropodomorph dinosaurs from the Löwenstein formation (Norian, Late Triassic) of Germany. Palaeontology, **46** (2), 317-337.

— 2003c. A definite prosauropod dinosaur from the Lower Elliot Formation (Norian: Upper Triassic) of South Africa. Palaeontologia Africana, **39**, 63-68.

— 2004. *Anchisaurus polyzelus* (Hitchcock): The Smallest Known Sauropod Dinosaur and the Evolution of Gigantism among Sauropodmorph Dinosaurs. Postilla, **230**, 1-58.

— 2007. Solving a dinosaurian puzzle: the identity of *Aliwalia rex* Galton. Historical Biology, **18** (4), 1-31.

— and KITCHING, J. W. 2003. The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. Proceedings of the Royal Society B: Biological Sciences, **270** (1525), 1753-1758.

— and VASCONCELOS, C. C. 2005. Furcula-like clavicles in the prosauropod dinosaur *Massospondylus*. Journal of Vertebrate Paleontology, **25** (2), 466-468.

—, HANCOX, P. J. and RUBIDGE, B. S. 2004. First record of a sauropod dinosaur from the upper Elliot Formation (Early Jurassic) of South Africa. South African Journal of Science, **100** (9-10), 504-506.

YE, Y., OUYANG, H. and FU, Q.-M. 2001. [New material of *Mamenchisaurus hochuanensis* from Zigong, Sichuan]. Vertebrata PalAsiatica, **39**, 266-271.

YOUNG, C.-C. 1939. On a new Sauropoda, with notes on other fragmentary reptiles from Szechuan. Bulletin of the Geological Society of China, **19**, 279-315.

— 1941. A complete osteology of *Lufengosaurus huenei* (gen. et sp. nov.) from Lufeng, Yunnan, China. Palaeontologica Sinica C, **7**, 1-53.

— 1942. *Yunnanosaurus huangii* (gen. et sp. nov.) a new Prosauropoda from the red beds at Lufeng, Yunnan. Bulletin of the Geological Society of China, **22**, 63-104.

— 1947. On *Lufengosaurus magnus* (sp. nov.) and additional finds of *Lufengosaurus huenei* Young. Palaeontologica Sinica (C), **12**, 1-53.

— 1958. New sauropods from China. Vertebrata PalAsiatica, **2**, 1-28.

ZARDOYA, R. and MEYER, A. 1998. Complete mitochondrial genome suggests diapsid affinities of turtles. Proceedings of the National Academy of Sciences, **95**, 14226-14231.

ZHANG, Y. 1988. [The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan: sauropod dinosaurs. Vol. 1, *Shunosaurus*]. Sichuan Publishing House of Science and Technology, Chengdu, 89 pp.

— and YANG, Z. 1995. [A complete osteology of prosauropoda in Lufeng Basin, Yunnan, China. *Jingshanosaurus*]. Yunnan Science and Technology Publishing House, Kunming, 100 pp.

—, YANG, D. and PENG, G. 1984. New Materials of *Shunosaurus* from Middle Jurassic of Dashanpu, Zigong, Sichuan. Journal of Chengdu College of Geology, **Supplement 2**, 1-12.

—, LI, K. and ZENG, Q. 1998. A new species of sauropod dinosaur from the Upper Jurassic of Sichuan Basin, China (*Mamenchisaurus jingyanensis* sp. nov.). Journal Chengdu University of Technology, **25** (1), 61-70.

ZHAO, X. 1993. A new mid-Jurassic sauropod (*Klamelisaurus gobiensis* gen. et sp. nov.) from Xinjiang, China. Vertebrata PalAsiatica, **31**, 132-138.

Appendix: Myological overview

	Muscle	Amphibia	Lepidosauria	Crocodylia	Aves
1	M. cucullaris	M. cucullaris (exoccipitals - cranial edge of scapula)	M. cucullaris / M. trapezius (cranial axial skeleton - acromial region of scapula) M. sternocleidomastoideus (occiput - clavicle, interclavicle, sternum)	M. cucullaris / M. trapezius (cranial axial skeleton - cranial edge of scapular blade) M. sternocleidomastoideus (occiput - sternum) M. sternoatlanticus (atlas - sternum)	M. cucullaris (occiput - furcula)
2	M. rhomboideus	**N/A**	**N/A**	M. rhomboideus (dorsal fascia - medial suprascapula)	M. rhomboideus superficialis (neural spines - dorsal edge of scapula)
3	M. levator scapulae	M. levator scapulae (occiput - suprascapula)	M. levator scapulae caput dorsalis (transverse processes of atlas/axis - suprascapula) M. levator scapulae caput ventralis (transverse processes of atlas/axis - cranial scapula)	M. levator scapulae (cervical ribs and transverse processes - cranial scapula)	**N/A**
4	M. serratus superficialis	M. serratus superficialis (reduced)	M. serratus superficialis (cervical and dorsal ribs - caudal edge of suprascapula)	M. serratus superficialis (uncinate processes - caudal edge of scapula)	M. serratus superficialis cranialis (cervicodorsal ribs - cranioventral scapula) M. serratus superficialis caudalis (thoracic ribs - caudoventral scapula)
5	M. serratus profundus	M. serratus profundus (cervical ribs - medial suprascapula)	M. serratus profundus (cervical ribs - medial suprascapula)	M. serratus profundus (cervical transverse processes - medial suprascapula, scapula)	M. serratus profundus (cervicodorsal ribs - caudomedial scapula) M. rhomboideus profundus (neural spines - dorsal edge of scapula)
6	M. costocoracoideus	M. sternohyoideus	M. costocoracoideus (first sternal rib - Lig. sternoscapulare internum)	M. costocoracoideus (last cervical and first sternal ribs - caudomedial coracoid)	**N/A**
7	M. sternocoracoideus		M. sternocoracoideus superficialis (craniodorsal sternum - medial coracoid) M. sternocoracoideus profundus (caudodorsal sternum - medial coracoid)	**N/A**	M. sternocoracoideus (sternocoracoidal process - Impressio m. sternocoracoidei)
8	M. deltoideus scapularis	M. deltoideus scapularis (lateral suprascapula - deltopectoral crest)	M. deltoideus scapularis (lateral suprascapula, scapula - deltopectoral crest)	M. deltoideus scapularis (lateral scapula - dorsocranial humerus)	**N/A**
9	M. deltoideus clavicularis	M. procoracohumeralis superficialis (craniolateral coracoid - cranial deltopectoral crest)	M. deltoideus clavicularis (lateral clavicle - cranial deltopectoral crest)	M. deltoideus clavicularis (cranioventral scapula - cranial deltopectoral crest)	M. deltoideus major (acromion process, furcula - cranial deltopectoral crest) M. deltoideus minor (area of triosseal foramen - cranial deltopectoral crest)
10	M. coracobrachialis	M. coracobrachialis brevis (caudoventral coracoid - proximoventral humerus) M. coracobrachialis longus (caudolateral angle of coracoid - entepicondyle)	M. coracobrachialis brevis (caudoventral coracoid - proximoventral humerus) M. coracobrachialis longus (caudolateral angle of coracoid - entepicondyle)	M. coracobrachialis brevis (lateral coracoid - proximoventral humerus) **N/A**	M. coracobrachialis cranialis (acrocoracoid process - Impressio coracobrachialis) **N/A**
11	M. supracoracoideus	M. supracoracoideus (ventral coracoid - apex of deltopectoral crest)	M. supracoracoideus (cranioventral coracoid - lateral tuberosity)	M. supracoracoideus caput scapularis (ventrolateral scapula - base of deltopectoral crest)	M. supracoracoideus (sternum, coracoid - lateral tuberosity)

				M. supracoracoideus caput coracoideum (cranial coracoid - apex of deltopectoral crest)	
12	M. pectoralis	M. pectoralis (sternum - caudal deltopectoral crest)	M. pectoralis (sternum, interclavicle, gastralia - caudal deltopectoral crest)	M. pectoralis (sternum, interclavicle, sternal ribs - caudal deltopectoral crest)	M. pectoralis (sternum, furcula - caudal deltopectoral crest)
13	M. latissimus dorsi	M. latissimus dorsi (dorsal fascia - dorsal humerus)	M. latissimus dorsi (dorsal fascia - dorsal humerus)	M. latissimus dorsi (dorsal fascia - dorsal humerus)	M. latissimus dorsi cranialis (cervicodorsal neural spines - caudal humerus) M. latissimus dorsi caudalis (caudal dorsal neural spines - caudal humerus)
14	M. teres major	**N/A**	**N/A**	M. teres major (caudolateral scapular blade - proximodorsal humerus)	**N/A**
15	Mm. scapulohumeralis	M. scapulohumeralis (ventral scapula - dorsal humerus)	M. scapulohumeralis cranialis (ventral scapulocoracoid - proximodorsal humerus) M. scapulohumeralis caudalis (*Sphenodon* only) (ventral scapula - distally on medial tuberosity)	**N/A** M. scapulohumeralis caudalis (ventrocaudolateral scapula - caudoproximal humerus)	M. scapulohumeralis cranialis (collum scapulae - proximodorsal humerus) M. scapulohumeralis caudalis (lateral scapular blade - medial tuberosity)
16	M. subcoracoscapularis	M. subcoracoscapularis (medial scapulocoracoid - medial tuberosity)	M. subscapularis (medial scapula - medial tuberosity) M. subcoracoideus (medial coracoid - medial tuberosity)	M. subscapularis (medial scapula - medial tuberosity) **N/A**	M. subscapularis (proximomedial scapula - medial tuberosity) M. subcoracoideus (medial coracoid - medial tuberosity) M. coracobrachialis caudalis (ventrolateral coracoid - medial tuberosity)
17	M. triceps brachii	M. triceps brachii caput scapulare (caudal scapula - olecranon) M. triceps brachii caput coracoideum (caudal corner of coracoid - olecranon) M. triceps brachii caput humerale laterale (craniodorsal humerus - olecranon) M. triceps brachii caput humerale mediale (caudodorsal humerus - olecranon)	M. triceps brachii caput scapulare (ventrolateral scapula - olecranon) M. triceps brachii caput coracoideum (caudomedial edge of coracoid - olecranon) M. triceps brachii caput humerale laterale (craniodorsal humerus - olecranon) M. triceps brachii caput humerale mediale (caudodorsal humerus - olecranon)	M. triceps brachii caput scapulare (caudoventral scapula - olecranon) M. triceps brachii caput coracoscapulare (Ligamentum sternoscapulare internum - olecranon) M. triceps brachii caput humerale laterale (craniodorsal humerus - olecranon) M. triceps brachii caput humerale mediale (caudal humerus - olecranon) M. triceps brachii caput humerale posticum (dorsal humerus - olecranon)	M. scapulotriceps (collum scapulae - olecranon) M. coracotriceps (sternocoracoidal ligament - olecranon) M. humerotriceps (caudodorsal humerus - olecranon)
18	M. biceps brachii	**N/A**	M. biceps brachii (ventromedial coracoid - cranioproximal ulna and radius)	M. biceps brachii (cranioventral coracoid - cranioproximal ulna and radius)	M. biceps brachii (acrocoracoid process, bicipital crest - ulna, radius)
19	M. humeroradialis	**N/A**	M. humeroradialis (*Sphenodon* only) (Lig. scapulohumerale laterale - M. supinator)	M. humeroradialis (craniodorsal humerus - proximolateral radius)	?M. deltiodeus propatagialis caput breve
20	M. brachialis	M. brachialis (proximal humerus - proximocranial radius)	M. brachialis (cranioventral humerus - cranioproximal ulna and radius)	M. brachialis (cranioventral humerus - cranioproximal ulna and radius)	M. brachialis (caudodistal humerus - proximoventral ulna)
21	M. supinator	M. extensor antebrachii et carpi radialis (distal ectepicondyle - cranial radius, radiale, intermedium)	M. supinator (proximal ectepicondyle - craniomedial radius)	M. supinator (ectepicondyle - craniomedial radius)	M. supinator (craniolateral ectepicondyle - dorsoproximal radius)
22	M. abductor radialis		M. abductor radialis (ventrodistal ectepicondyle - craniolateral radius)	M. abductor radialis (ventrodistal ectepicondyle - proximolateral radius)	**N/A**
23	M. ectepicondylo-ulnaris	M. extensor antebrachii et carpi ulnaris (distal ectepicondyle - lateral ulna, ulnare, pisiforme)	M. ectepicondylo-ulnaris (*Sphenodon* only) (distal ectepicondyle - proximal ulna)	M. ectepicondylo-ulnaris (M. flexor ulnaris) (distal ectepicondyle - lateral ulna)	M. ectepicondylo-ulnaris (distal ectepicondyle - proximodorsocranial ulna)
24	M. pronator teres	M. flexor antebrachii et carpi radialis (entepicondyle - radius)	M. pronator teres (entepicondyle - cranial radius)	M. pronator teres (entepicondyle - cranial radius)	M. pronator superficialis (entepicondyle - ventral radius) M. pronator profundus (entepicondyle - caudoventral radius)

25	M. entepicondylo-ulnaris	M. epitrochleo-anconaeus (entepicondyle - medial ulna)	M. entepicondylo-ulnaris (entepicondyle - medial ulna)	**N/A**	M. entepicondylo-ulnaris (Galloanserae only) (craniodistal entepicondyle - caudoventral ulna)
26	M. pronator quadratus	M. pronator quadratus (lateral ulna - medial radius)	M. pronator quadratus (lateral ulna - medial radius) M. pronator accessorius (entepicondyle - proximal radius)	M. pronator quadratus (lateral ulna - medial radius)	M. ulnometacarpalis ventralis (ventral ulna - craniodorsal carpometacarpus)
27	M. extensor carpi radialis	M. extensor antebrachii et carpi radialis (distal ectepicondyle - cranial radius, radiale, intermedium)	M. extensor carpi radialis (central ectepicondyle - cranial radius, radiale)	M. extensor carpi radialis (central ectepicondyle - radiale)	M. extensor carpi radialis (cranial ectepicondyle - carpometacarpal extensor process)
28	M. extensor carpi ulnaris	M. extensor antebrachii et carpi ulnaris (distal ectepicondyle - lateral ulna, ulnare, pisiforme)	M. extensor carpi ulnaris (distal ectepicondyle - pisiforme, metacarpal V)	**N/A**	M. extensor carpi ulnaris (distal ectepicondyle - intermetacarpal process)
29	M. supinator manus	M. supinator manus (proximal carpus - proximomedial metacarpal I)	M. supinator manus (distomedial ulna - proximomedial metacarpal I)	M. supinator manus (lateral radius, medial ulna - radiale)	M. extensor longus alulae (radius, ulna - carpometacarpal extensor process)
30	M. extensor digitorum communis	M. extensor digitorum communis (dorsal ectepicondyle - distal phalanges)	M. extensor digitorum communis (dorsal ectepicondyle - proximolateral metacarpals I-IV)	M. extensor digitorum communis (ectepicondyle - proximal metacarpals II and III) M. extensor metacarpi I (radiale - proximal metacarpal I) M. extensor metacarpi IV (ulnare - proximal metacarpal IV)	M. extensor digitorum communis (ectepicondyle - proximal phalanges dig. I + II)
31	M. flexor carpi radialis	M. flexor antebrachii et carpi radialis (entepicondyle - radius)	M. flexor carpi radialis (ventral entepicondyle - medial radiale, distal carpus)	**N/A**	**N/A**
32	M. flexor carpi ulnaris	M. flexor carpi ulnaris (entepicondyle - ventral pisiforme)	M. flexor carpi ulnaris (entepicondyle - ventral pisiforme)	M. flexor carpi ulnaris (entepicondyle - ventral pisiforme)	M. flexor carpi ulnaris (entepicondyle - processus muscularis of the ulnare)
33	M. flexor digitorum longus	M. flexor digitorum longus (entepicondyle, distal ulna - terminal phalanges)	M. flexor digitorum longus (entepicondyle, ulna, ulnare - terminal phalanges)	M. flexor digitorum longus (entepicondyle, ulna - terminal phalanges dig. I-III)	M. flexor digitorum superficialis (entepicondyle - proximal phalanx dig. II) M. flexor digitorum profundus (ventral ulna - terminal phalanx dig. II)
34	Mm. extensores digitorum superficiales	Mm. extensores digitorum superficiales (dorsal proximal carpus - distal phalanges)	Mm. extensores digitorum superficiales (dorsal proximal carpus - terminal phalanges)	Mm. extensores digitorum superficiales (dorsal proximal carpus - terminal phalanges)	M. extensor longus digiti majoris (caudal radius - terminal phalanx dig. II) M. ulnometacarpalis dorsalis (dorsodistal ulna - caudodorsal metacarpal III)
35	Mm. extensores digitorum profundes	Mm. extensores digitorum profundi (dorsal distal carpus - terminal phalanges)	Mm. extensores digitorum profundi (dorsal distal carpus - metacarpal-phalangeal joints)	Mm. extensores digitorum profundi (dorsal distal carpus - terminal phalanges)	M. extensor longus digiti majoris pars distalis (dorsal metacarpal II - terminal phalanx dig. II) M. extensor brevis alulae (craniodorsal metacarpal I - proximal pollex)
36	M. abductor pollicis brevis	**N/A**	M. abductor pollicis brevis (ventromedial radiale - proximomedial on phalanx I.1)	M. abductor pollicis brevis (ventromedial radiale - proximomedial metacarpal I)	M. abductor alulae (extensor tendon - cranioventral phalanx I.1)
37	M. abductor digiti V	**N/A**	M. abductor digiti V (pisiforme - lateral phalanx V.1)	M. abductor digiti V (pisiforme - lateral metacarpal V)	**N/A**
38	Mm. flexores digitorum superficiales	Mm. flexores digitorum superficiales (dorsal palmar aponeurosis - distal metacarpals, phalanges)	Mm. flexores digitorum superficiales (ventral palmar aponeurosis - ungual flexor tubercles)	Mm. flexores digitorum superficiales (ventral palmar aponeurosis - ventral proximal phalanges)	**N/A**
39	M. flexor pollicis brevis	**N/A**	M. flexor pollicis brevis (distal carpals - proximal phalanx I.1)	**N/A**	M. flexor alulae (proximal carpometacarpus - proximal pollex)
40	M. flexor digiti V	**N/A**	M. flexor digiti V (distal carpals - proximomedial phalanx V.1)	M. flexor digiti V, M. transversus palmaris (radiale - ventromedial metacarpal V, phalanges)	**N/A**
41	Mm. lumbricales	**N/A**	Mm. lumbricales (dorsal palmar aponeurosis - proximal phalanges II-IV)	Mm. lumbricales (dorsal palmar aponeurosis - proximal phalanges II-IV)	**N/A**

42	Mm. flexores digitorum profundi	Mm. flexores digitorum profundi (distal carpals - ventral metacarpals)	Mm. flexores digitorum profundi (distal carpals - proximal phalanges)	Mm. flexores digitorum profundi (metacarpals - proximal phalanges)	M. abductor digiti majoris (ventral metacarpal II - proximal phalanx II) M. flexor digiti minoris (ventral metacarpal III - proximal phalanx III)
43	Mm. interossei	Mm. interossei (between metacarpals)	Mm. interossei (between metacarpals)	Mm. interossei (between metacarpals)	?M. adductor alulae (cranial metacarpal II - caudal digit I)

Lebenslauf

Persönliche Angaben

Name: Kristian Remes
Anschrift: Bornheimer Straße 93
53119 Bonn
Geburtsdatum: 04.12.1978
Geburtsort: Detmold
Staatsangehörigkeit: deutsch
Familienstand: verheiratet

Ausbildung

2004	Diplom im Studiengang Geologie/Paläontologie, FU Berlin
2003	Diplomarbeit an der FU Berlin und am Museum für Naturkunde, Thema: „Revision von *‚Barosaurus' africanus* (Sauropoda, Diplodocinae) aus den Tendaguru-Schichten Tansanias“
	Diplomkartierung und paläontologische Prospektion im Raum Cruzy, Dept. Hérault, Frankreich
1998	Abitur am Christian-Dietrich-Grabbe-Gymnasium, Detmold

Berufserfahrung

Anstellungen:

seit Oktober 2007	wiss. Mitarbeiter am Institut für Paläontologie, Rheinische Friedrich-Wilhelms-Universität Bonn
2006 – Juli 2007	wiss. Mitarbeiter (DFG) am Museum für Naturkunde
2005 – 2006	wiss. Angestellter (DFG) an der Bayerischen Staatssammlung für Paläontologie und Geologie, München
2004	wiss. Mitarbeiter (DFG) am Museum für Naturkunde
2001 – 2004	Sammlungstutor in der FR Paläontologie, FU Berlin
2001	studentische Hilfskraft am Deutschen Zentrum für Luft- und Raumfahrt e.V., Berlin-Adlershof

Auslandsaufenthalte:

2004 – 2006	Forschungsarbeiten zur Dissertation in Großbritannien, Frankreich, Indien, China, Südafrika, Brasilien, Argentinien und den USA, Gesamtdauer ca. 5 Monate

Eingeworbene Drittmittel:

beantragt ab April 2008	DFG-gefördertes Projekt „Ontogeny and Phylogenetic Relationships of *Europasaurus holgeri* (Macronaria, Sauropoda)“
2005	EU Synthesys-Projekt FR-TAF-730 (MNHN, Paris)
	Doris and Samuel P. Welles Fund (UCMP, Berkeley, California)

Geländearbeiten:

2004	paläontologische Prospektion und Grabung in Chubut, Patagonien, Argentinien (Projekt O. Rauhut)
2003	geologische Kartierung und paläontologische Prospektion in Hérault, Frankreich (2 Monate)
2002	paläontologische Grabung in Espéraza, Aude, Frankreich (1 Monat, Projekt Musée des Dinosaures)

Lehrerfahrungen:

2002 – 2004	Beteiligung an Vorlesungen und Oberseminaren in der FR Paläontologie, FU Berlin (Osteologie der Wirbeltiere, Paläontologie der Vertebraten, Paläontologie für Nebenfächler)
1999 – 2002	Organisation und Durchführung geologisch-paläontologischer Exkursionen für Studienanfänger

Preise:

2005	Katharina-Heinroth-Preis der Gesellschaft naturforschender Freunde zu Berlin e.V. für eine herausragende Diplomarbeit in den Lebenswissenschaften

Mitgliedschaften:	Society of Vertebrate Paleontology, Palaeontological Association, Paläontologische Gesellschaft, European Association of Vertebrate Paleontologists

Öffentlichkeitsarbeit

2005 – 2007	Lange Nacht der Wissenschaften sowie Sonntags- und Abendveranstaltungen am Museum für Naturkunde

Ausstellungen:

2005-2007	wissenschaftliche Betreuung der neuen Dinosaurier-Ausstellung (Skelettrekonstruktionen, Texte, Bilder, Animationen) im Rahmen der Teilerneuerung der Ausstellungen des Museums für Naturkunde (Evolution in Aktion – EFRE-Projekt)

Medienpräsenz:

2003 – 2007	Print:	Süddeutsche Zeitung, Abendzeitung München, Tchibo TV Magazin, Berliner Morgenpost,

Die Welt, Tagesspiegel, Berliner Zeitung, ddp, dpa,
Neues Deutschland, Die Zeit, WAZ, GEO, reuters
Radio: BB Radio, Radio NDR 4, Bayern2 Radio,
RBB Kultur Radio, RBB radio eins, Spreeradio,
Radio Teddy, Deutschlandfunk, Deutschlandradio
TV: RBB, ARD (W wie Wissen), ZDF Morgenmagazin,
BBC, reuters TV, Deutsche Welle, Bahn TV,
Pro7 (Focus TV), RTL II, VOX, ap, FAB

Publikationen

Papers:

REMES, K. 2007a. A second Gondwanan diplodocid dinosaur (Sauropoda, Diplodocoidea) from the Upper Jurassic Tendaguru Beds of Tanzania, East Africa. Palaeontology, 50 (3), 653-667.

REMES, K. 2007b. Revision von *"Barosaurus" africanus*: Die Diplodociden vom Tendaguru. Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin, (N.F.) 45, 55-64.

REMES, K. 2007c. Baupläne für Riesen. Humboldt-Spektrum, 2007 (2), 18-21.

REMES, K. 2006a. Revision of the Tendaguru sauropod *Tornieria africana* (Fraas) and its relevance for sauropod paleobiogeography. Journal of Vertebrate Paleontology, 26 (3), 651-669.

RAUHUT, O. W. M., REMES, K., FECHNER, R., CLADERA, G. and PUERTA, P. 2005. Discovery of a short-necked sauropod dinosaur from the Late Jurassic of Patagonia. Nature, 435, 670-672.

Publizierte Abstracts:

REMES, K. 2006b. Evolution of forelimb functional morphology in sauropodomorph dinosaurs. Journal of Vertebrate Paleontology, 26 (3 suppl.), 115A.

REMES, K. 2006c. Quadrupedal locomotion in prosauropods and the transition to sauropods. 6. *In* CHO, H.-H. (ed). 2nd GNHM Symposium on the evolution of life. GNHM, Daejeon, South Korea.

REMES, K. and RAUHUT, O. 2005a. New Insights into the Origin and Evolution of Diplodocoid Sauropods. Journal of Vertebrate Paleontology, 25 (3 suppl.), 104A.

REMES, K. and RAUHUT, O. 2005b. The oldest Indian dinosaur *Alwalkeria maleriensis* revised: A chimera including remains of a basal saurischian. *In* KELLNER, A. W. A., HENRIQUES, D. D. R. and RODRIGUES, T. (eds). Boletim de resumos - II Congresso Latino-Americano de Paleontologia de Vertebrados, Rio de Janeiro, RJ, Brasil, 10 a 12 de agosto de 2005. Museu Nacional, Rio de Janeiro.

REMES, K. 2004a. The Tendaguru sauropod *"Barosaurus" africanus* and the paleobiogeography of diplodocid sauropods. 23-24. In EVANS, M. and FORREST, R. (eds). 52nd Symposium of Vertebrate Palaeontology and Comparative Anatomy, Abstracts. University of Leicester, Leicester.

REMES, K. 2004b. Der Tendaguru-Sauropode *"Barosaurus" africanus* und die Paläobiogeographie der Diplodocidae (Sauropoda). 195-196. *In* REITNER, J., REICH, M. and SCHMIDT, G. (eds). Geobiologie. 74. Jahrestagung der Paläontologischen Gesellschaft, Göttingen, 02. bis 08. Oktober 2004. Kurzfassungen der Vorträge und Poster. Universitätsverlag Göttingen, Göttingen.