Osteology of *Cryolophosaurus ellioti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution

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Cryolophosaurus ellioti Hammer and Hickerson, 1994, from the Early Jurassic Hanson Formation of the Central Transantarctic Mountains, represents a theropod dinosaur from a period of time and geographical area that are poorly sampled with respect to dinosaur taxa. An in-depth morphological description of *Cryolophosaurus* is presented here, along with a rigorous phylogenetic analysis of theropod relationships consisting of 347 characters and 56 taxa, in an attempt to clarify the relationships of *Cryolophosaurus* and to provide insight into questions surrounding early theropod evolution. *Cryolophosaurus* is characterized by a unique cranial crest, formed primarily by the lacrimals, a pronounced constriction of the squamosal and jugal bones across the infratemporal fenestra, and extremely elongate cranial processes on the cervical ribs. Several shared characters, including the presence of a slot-shaped foramen at the base of the nasal process of the premaxilla, nasolacrimal crests and erect tab-like dorsal processes on the articular, suggest affinities between *Cryolophosaurus* and a clade of medium-bodied Early Jurassic theropods that includes '*Dilophosaurus*' *sinensis*, *Dracovenator regenti* and *Dilophosaurus wetherilli*. This clade is recovered as sister-taxon to a Neoceratosauria + Tetanurae clade, rendering both a traditional Coelophysoidea and Ceratosauria non-monophyletic. *Cryolophosaurus* represents the largest known Early Jurassic theropod, and marks the beginning of theropod occupation of the dominant predator niche in the Mesozoic.   © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **151**, 377–421.

ADDITIONAL KEYWORDS: *Cryolophosaurus* – Gondwana – Hanson Formation – Lower Jurassic – phylogeny.

INTRODUCTION

The theropod dinosaur *Cryolophosaurus ellioti* (Hammer & Hickerson, 1994) is the most complete dinosaur yet discovered in Antarctica, and is unique in several of its biological attributes. At an estimated 6.5 m in body length and 465 kg, *Cryolophosaurus* represents the largest theropod known from the Early Jurassic. In appearance, it is distinguished from all other theropods in the possession of a distinct crest fromed by transversely expanded dorsal rami of the lacrimals, as well as the nasals. Despite its relative completeness, a detailed account of the morphology of *Cryolophosaurus* is lacking, and its phylogenetic affinities have remained relatively obscure.

Early phylogenetic analyses of Theropoda indicated that the clade consisted of two monophyletic groups: Ceratosauria and Tetanurae (Gauthier, 1986; Rowe & Gauthier, 1990). When first discovered, *Cryolophosaurus* was considered a derived tetanuran whose relatives were Late Jurassic or younger in age (Hammer & Hickerson, 1994; Sereno *et al*., 1996). However, other

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authors have suggested that *Cryolophosaurus* may occupy a more basal position in theropod phylogeny, recovering this taxon as the sister group to all other Tetanurae (Carrano & Sampson, 2003; Smith, Hammer & Currie, 2005). Many of these recent studies (Rauhut, 1998, 2003; Carrano & Sampson, 1999, 2003; Forster, 1999; Carrano, Sampson & Forster, 2002; Carrano, Hutchinson & Sampson, 2005; Wilson *et al.*, 2003; Sereno, Wilson & Conrad, 2004; Smith *et al.*, 2005; Yates, 2005) have also suggested that Ceratosauria represents a paraphyletic group, usually proposing that Coelophysoidea and Neoceratosauria are successive sister-taxa to Tetanurae. Conversely, analyses by Tykoski & Rowe (2004) and Tykoski (2005) recover a traditional Ceratosauria, and suggest that the paraphyletic Ceratosauria recovered in recent analyses may be a consequence of either incorrectly scoring characters that are ontogenetically variable, or a priori omission of ontogeny-dependent characters. In addition to these discrepancies, several studies have called into question the monophyly of a traditional Coelophysoidea (Carrano, Sampson & Forster, 2002; Rauhut, 2003; Yates, 2005). These studies range from simply recovering one member of Coelophysoidea, *Dilophosaurus wetherilli*, as more closely related to neoceratosaurs and tetanurans (Carrano *et al.*, 2002; Rauhut, 2003), to proposing the existence of a novel clade of early theropods (including *Dilophosaurus wetherilli*) that represents the sister-taxon to Neoceratosauria + Tetanurae (Yates, 2005). This latter hypothesis suggests that theropods passed through a 'coelophysoid' stage in their early evolution (Yates, 2005). Thus, it is clear that basal theropod phylogeny is currently in a state of revision. Incorporation of information from the Early Jurassic theropod *Cryolophosaurus ellioti* (Hammer & Hickerson, 1994), which seems to share numerous characteristics with coelophysoids, neoceratosaurs and tetanurans, sheds additional light on this debate.

Cryolophosaurus is also known from a period of geological time, the Early Jurassic, which is particularly interesting with regard to theropod evolution. Several studies suggest that the early Middle Jurassic was a critical period of early theropod diversification (Allain, 2002; Carrano, Hutchinson & Sampson, 2005; Rauhut, 2005a). As Rauhut (2005a: 107) noted, tetanuran diversification was well underway by the Bathonian, with basal representatives from several major lineages present, including the spinosauroids *Eustreptospondylus* and *Dubreuillosaurus*, the coelurosaur *Proceratosaurus*, and the allosauroid *Monolophosaurus* (Sereno, 1999; Holtz, 2000; Allain, 2002; Rauhut, 2003). The oldest definitive members of Tetanurae currently known are *Magnosaurus nethercombensis* and '*Megalosaurus*' *hesperis* from the Aalenian–Bajocian (early Middle Jurassic) of England (Waldman, 1974;

Holtz, 2000; Rauhut, 2003, 2005a). The oldest definitive members of Neoceratosauria, *Ceratosaurus* and *Elaphrosaurus*, do not appear until even later, in the Late Jurassic. However, the fragmentary theropod *Ozraptor subotaii* (which may represent the oldest known member of Abelisauroidea) and two undescribed neoceratosaur species from the Middle–Late Jurassic Shishugou Formation of China may extend the earliest record of Neoceratosauria (Rauhut, 2005b; Xu & Clark, 2006). Besides *Cryolophosaurus*, only four possible non-coelophysoid theropods are currently known from the Early Jurassic. One is the fragmentary *Eshanosaurus deguchiianus* from the Lower Jurassic of China (Xu, Zhao & Clark, 2001). This taxon is purported to be a therizinosaur (Xu *et al.*, 2001), but may instead represent a prosauropod dinosaur (Rauhut, 2003). A partial left foot from the Toarcian of North Africa has also tentatively been referred to Coelurosauria (Jenny *et al.*, 1980; Taquet, 1985; Allain, 2002). '*Dilophosaurus*' *sinensis*, from the lower Lufeng Formation of China, was recently described by Hu (1993) as being congeneric with the North American *Dilophosaurus wetherilli*, though this generic assignment, and the taxon's status as a coelophysoid, has been questioned (Lamanna *et al.*, 1998; Rauhut, 2003; Carrano & Sampson, 2004). In addition, a theropod knee joint originally included in the holotype of *Scelidosaurus harrisonii* probably represents a basal tetanuran, though no more specific diagnosis for this specimen has been advanced (Newman, 1968; Carrano & Sampson, 2004). Coelophysoids appear to have remained diverse morphologically and geographically through the end of the Early Jurassic, though no coelophysoids younger than the Toarcian are currently known (Carrano & Sampson, 2004; Carrano *et al.*, 2005). Coupled with the fact that more derived theropods remain relatively unknown in the Early Jurassic, yet appear to have diversified considerably by the end of the Middle Jurassic, this suggests that this interval of time represents a focal period of reorganization of theropod communities (Carrano & Sampson, 2004). The accurate phylogenetic placement of *Cryolophosaurus* can fill a critical gap in theropod evolutionary history, and also offer a means of testing previous hypotheses of the tempo of early theropod diversification.

The paucity of theropod material from the Antarctic continent also makes *Cryolophosaurus* valuable in a biogeographical context. Molnar, Angriman & Gasparini (1996) referred fragmentary remains from the Cretaceous of Antarctica to Theropoda. More recently, a field party led by Jim Martin of the South Dakota School of Mines and Technology and Judd Case of Saint Mary's College of California reported the discovery of a theropod dinosaur from Late Cretaceous marine sediments on the Antarctic peninsula. These

two specimens, along with the *Cryolophosaurus* material, comprise the entirety of the non-avian theropod record from the Mesozoic of Antarctica. A detailed understanding of *Cryolophosaurus* will not only aid in learning more about the evolution of the Antarctic fauna through the Mesozoic, but, placed in a phylogenetic context, could ultimately provide tests of biogeographical scenarios involving the Antarctic continent in the Early Jurassic.

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York; BMNH, British Museum of Natural History, London; FMNH, Field Museum of Natural History, Chicago; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires; MB, Museum für Naturkunde der Humboldt Universität, Berlin; MCF-PVPH, Museo Carmen Funes, Palaeontología Vertebrados, Plaza Huincul; MNHN, Muséum National d'Histoire Naturelle, Paris; MNN, Musée National du Niger, Niamey; MPEF, Museo Palaeontológico Egidio Feruglio, Trelew; MUCPv, Museo de la Universidad Nacional del Comahue, Neuquén; MUCPv-CH, Museo de la Universidad Nacional del Comahue, El Chocón collection, Neuquén; MWC, Museum of Western Colorado, Fruita; PULR, Palaeontología, Universidad de La Rioja; PVL, Fundación Miguel Lillo, San Miguel de Tucumán; PVSJ, Museo Provincial de San Juan, San Juan; QG, Queen Victoria Museum, Salisbury, Zimbabwe; TMM, Texas Memorial Museum, Austin; YPM, Yale Peabody Museum, New Haven.

ANATOMICAL ABBREVIATIONS USED IN FIGURES

4t, fourth trochanter; acpl, anterior centroparapophyseal lamina; ahg, anterior horizontal groove; alvr, alveolar ridge; ang, angular; aof, antorbital fenestra; ap, astragalar ascending process; art, articular; ast, astragalus; ca, calcaneum; capt, capitulum; cc, cnemial crest; c. rib, cervical rib; crp, cranial process; crpl, centroprezygapophyseal lamina; cu, cultriform process; c. vert, cervical vertebra; cr. int, crista interfenestralis; crs, crest; dia, diapophysis; dd, dorsal depression on the prootic; dmg, damage from caudal vertebrae removal; dp, dorsal process; ecc, ectepicondyle; ect, ectopterygoid; emf, external mandibular fenestra; enc, entepicondyle; epi, epipterygoid; exo, exocciptial; fc, fibular condyle; fen. ova, fenestra ovalis; fen. psd, fenestra pseudorotunda; fi, fibula; fos, fossa; fr, frontal; fr sut., interfrontal suture; gr, groove; hh, humeral head; hyp, hyposphene; int, internal tuberosity; is, ischium; is bt, ischial 'boot'; is ped, ischial peduncle; is rug, ischial rugosity; it, incisura

tibialis; itf, intertemporal fenestra; jug, jugal; la, lacrimal; la rec, lacrimal recess; lat, laterosphenoid; lat brv, lateral brevis shelf; lc, lateral condyle; lt, lesser (anterior) trochanter; mb, medial buttress; mec, medial epicondylar crest; mp, pendant medial process; mr, medial ridge; ms, metotic strut; mtx, matrix; mx, maxilla; na, nasal; nc, neural canal; ncs, neurocentral suture; ng, nutrient groove; ns, neural spine; ob fo, obturator foramen; olc, olecranon process; orb, orbit; pa, proximal articular surface; pag, proximal articular groove; par, parietal; para, parapophysis; pcdl, posterior centrodiapophyseal lamina; pg, posterior intercondylar groove; pl, pleurocoel; po, postorbital; podl, postzygadiapophyseal lamina; pos, postspinal fossa; poz, postzygapophysis; ppdl, paradiapophyseal lamina; prdl, prezygadiapophyseal lamina; pro, prootic; proc ob, obuturator process; prpl, prezygaparapophyseal lamina; prz, prezygapophysis; ps, proximal sulcus; pty. q, pterygoid flange of quadrate; qj, quadratojugal; ra tub, radial tuberosity; rdg, ridge; rt, right; sac, supracetabular crest; soc, supraoccipital; spl, splint of bone on fibula; spol, spinopostzygapophyseal lamina; sq, squamosal; sr, sacral rib; stf, supratemporal fenestra; sur, surangular; tc, tibial condyle; tfc, tibio-fibular crest; ti, tibia; to, tooth; trp, transverse process; tub, tuberculum; V, opening for trigeminal (CN V) nerve; V1, sulcus for ophthalmic branch of the trigeminal (CN V) nerve; VII, opening for facial (CN VII) nerve;

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA OWEN, 1842
SAURISCHIA SEELEY, 1887
THEROPODA MARSH, 1881
CRYOLOPHOSAURUS ELLIOTI HAMMER &
HICKERSON, 1994

Holotype: FMNH PR1821: nearly complete skull and associated partial skeleton.

Type locality and horizon: All material is from a single locality in the lower part of the exposures of the Hanson Formation on Mt. Kirkpatrick, in the Beardmore Glacier region of the Central Transantarctic Mountains, Antarctica. Elliot (1996) attributed an Early Jurassic age to the Hanson Formation.

Formerly the uppermost section of the Falla Formation, the Hanson Formation was erected in 1996 to differentiate the lower volcanic-poor portion of the Falla Formation from the upper volcaniclastic, tuffaceous section (Elliot, 1996; Figs 1D, 2). The Hanson Formation was deposited in an active volcanic–tectonic rift system formed during the breakup of Gondwana (Elliot, 1992, 1996; Elliot & Larsen, 1993). During the austral summer of 1990–1991, a vertebrate fossil
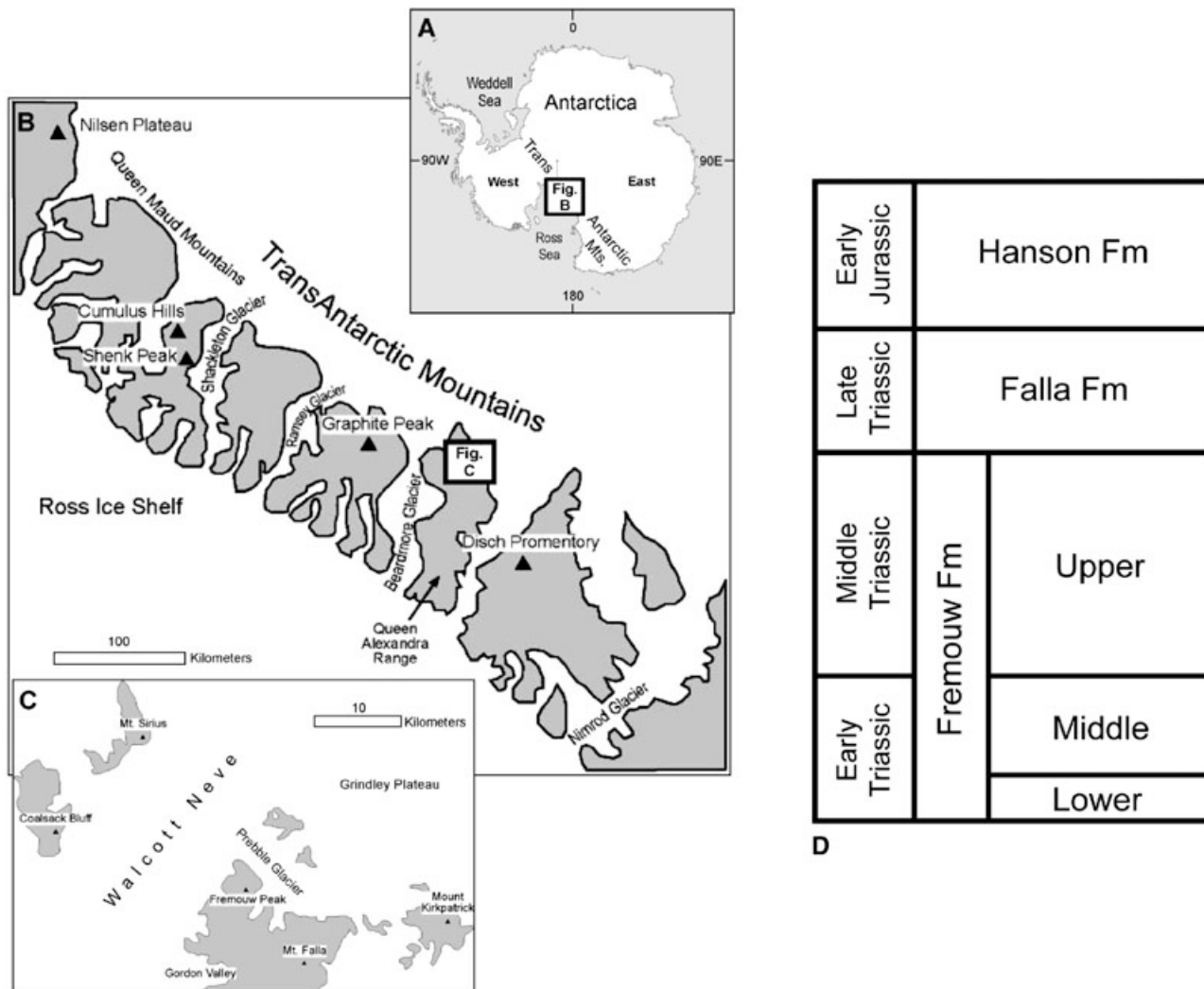
Figure 1. Generalized map of Antarctica (A), with inset maps showing the Central Transantarctic Mountains (B), and the Beardmore Glacier area where the Mount Kirkpatrick dinosaur site is located (C). D, generalized stratigraphy and age of rock units in the Beardmore Glacier area.

locality was discovered on Mt. Kirkpatrick in the Beardmore Glacier region of the Central Transantarctic Mountains (Fig. 1C). The site is at an altitude of approximately 4100 m in the tuffaceous siltstones and mudstones of the lower part of the Hanson Formation. Elements from at least seven different taxa were collected from the site during the 1990–91 and 2003–04 field seasons. This assemblage includes the relatively complete theropod dinosaur *Cryolophosaurus ellioti* (Hammer & Hickerson, 1994), distal limb elements from a basal sauropodomorph dinosaur, a pelvis and several postcranial elements from a possible sauropod dinosaur, the humerus of a rhamphorhynchoid pterosaur, and the tooth of a large tritylodont (Hammer & Hickerson, 1994). A minimum age for the site is established by basalt flows occurring above, and intruding into, fractures in the vertebrate-bearing sediments.

These diabase intrusions have been $^{40}Ar/^{39}Ar$ dated at 177 Ma (Heimann *et al.*, 1994). A maximum age is set by a *Dicroidium* fauna that occurs approximately 300 m below the vertebrate-bearing sediments in the Falla Formation. The presence of *Dicroidium odontopteroides* suggests a Late Triassic Age, and pollen and spore assemblages from the middle part of the Falla Formation have been assigned a Carnian to Norian age (Kyle & Schopf, 1982; Farabee, Taylor & Taylor, 1989; Elliot, 1996). Elliot (1996: 393) also notes that more specific dates have been recovered for the Hanson Formation, citing a trachyte pebble from the top of the sandstone–carbonaceous shale sequence which gives a K–Ar date of 203 ± 2 Ma (Barrett & Elliot, 1972), and a Rb–Sr isochron date of 186 ± 9 Ma for five tuffs from the upper part of the formation (Faure & Hill, 1973).

Beardmore Glacier Region
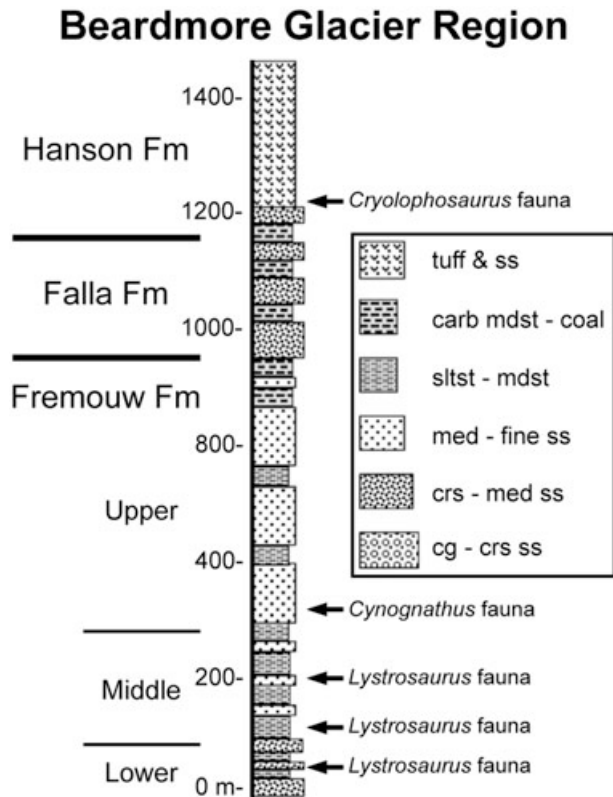
Figure 2. Detailed stratigraphy of the Fremouw, Falla and Hanson Formations in the Beardmore Glacier region. Several important vertebrate faunas are indicated. Rock unit legend abbreviations: carb, carbonaceous; cg, conglomorate; crs, coarse; Fm, Formation; med, medium; mdst, mudstone; sltst, siltstone; ss, sandstone.

Diagnosis: Theropod dinosaur distinguished from all other known theropods by the presence of a large, anterodorsally curving midline crest with fluted rostral and caudal surfaces formed by dorsal expansions of the lacrimals, a complete constriction across the infratemporal fenestra formed by the squamosal and jugal, and extremely elongate cranial processes on the cervical ribs. Selected measurements are given in Table 1.

ANATOMICAL DESCRIPTION

SKULL

A fragment of the left maxilla of *Cryolophosaurus* preserves the posteriormost three teeth (Fig. 3A, B). The teeth are inset slightly on the medial side of the maxilla, producing a small ledge on the medial alveolar border. This ledge is deeper and more distinct over the anteriormost tooth. It thins mediolaterally and blends smoothly into the medial surface of the maxilla posterior to the last tooth. A fragment of the right maxilla contains portions of at least six teeth (Fig. 3C). A rod-like ridge is present on the lateral side

Table 1. Selected measurements of *Cryolophosaurus ellioti* (FMNH PR1821). All measurements are given in millimetres. Measurements of elements that are incompletely preserved are denoted with an asterisk

Element	Measurement (mm)
Skull a-p length	460*
Skull d-v height	405
Skull, right orbit d-v height	190
Cervical 7 a-p length	118
Cervical 8 a-p length	108
Mid/post Dorsal (-D7-13) a-p length	114
1st articulated mid/post Dorsal (> D9) a-p length	125*
2nd articulated mid/post Dorsal (> D9) a-p length	115*
Posterior Dorsal (-D14) a-p length	117
Caudosacral 1 (=S5) a-p length	89
Anterior mid-caudal a-p length	100
Left ilium d-v height	204
Left pubis length	> 345
Left ischium length	> 520
Left femur length	769

and is similar in morphology to the alveolar ridges of many coelophysoids.

The posterior portions of both nasals are preserved (Figs 4–6). The dorsal midline suture between the nasals is straight (Fig. 6). The nasals are unfused, and each forms a pronounced, long, high ridge at roughly a 45 angle to the sagittal plane, giving them an emarginated V shape in dorsal view. The dorsal edges of the lateral ridges of the nasals are smooth and rounded. The dorsal portion of the antorbital fossa extends onto the lateroventral side of the nasals as in several allosauroids (*sensu* Currie & Zhao, 1994a), but also *Dilophosaurus wetherilli* (R. Tykoski, pers. comm. 2005). Pneumatic foramina are absent from the nasals. The nasals contribute only slightly to the medialmost portion of the base of the distinctive crest. The lateral ridges of the nasals turn medially at their posterior ends, converging on each other and becoming pinched between the dorsal expansions of the lacrimals at the base of the crest (Fig. 7). A similar condition is present in *Monolophosaurus* (Zhao & Currie, 1994). As the lateral ridges of the nasals become pinched medially between the lacrimals, they leave a small proximal gap at their posterior ends, below the base of the crest (Fig. 7). The nasals are separated from each other posteriorly by a long, narrow anterior wedge formed by the articulated frontals.

The right lacrimal is the better-preserved of the two, and the lacrimal body has an inverted L shape in lateral view as in most theropods (Fig. 4). The lacrimal
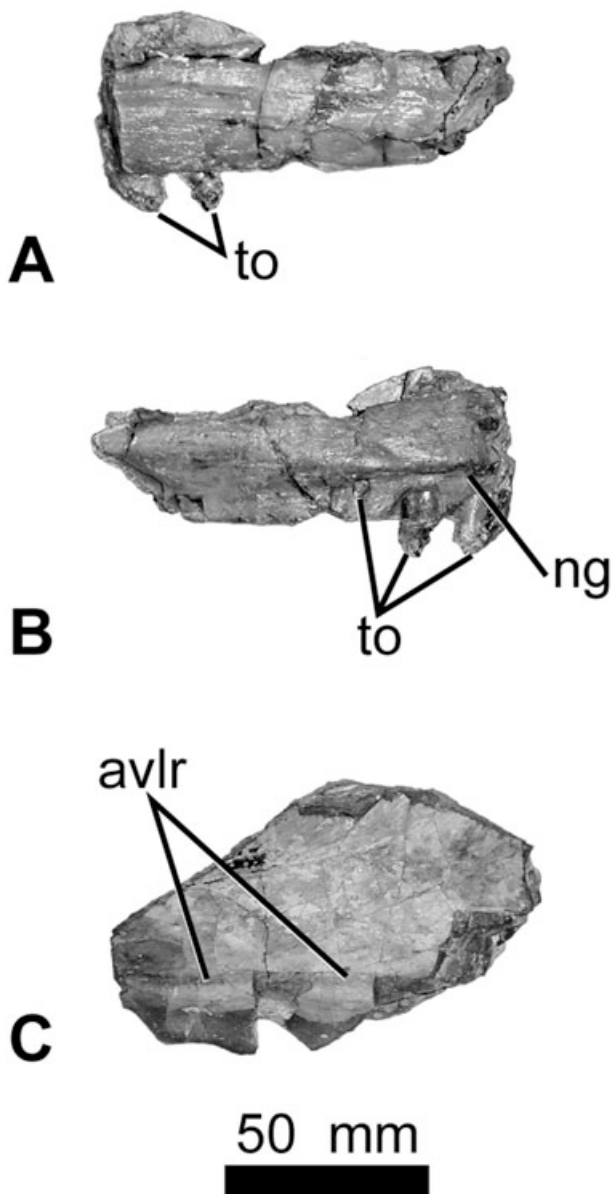
Figure 3. Left maxilla of *Cryolophosaurus ellioti* in lateral (A), and medial (B), aspects. Right maxilla of *Cryolophosaurus ellioti* in lateral (C) aspect.

also bears an expanded dorsal wing that is exposed on the skull roof as a transverse crest curving anterodorsally. This is similar to the condition in *Dilophosaurus wetherilli* (UCMP 77270), '*Dilophosaurus*' *sinensis* (Hu, 1993) and *Monolophosaurus* (Zhao & Currie, 1994), where the posterodorsal portion of the lacrimal contributes to a large crest. The lacrimal is dorsoventrally elongate and as tall as the orbit, contacting the jugal at the anteroventral margin of the orbit. The ventral portion of the lacrimal is broadly expanded anteroposteriorly at its contact with the jugal. The lac-

rimals fan out dorsally and curl anterodorsally distally to contribute to the large cranial crest (Fig. 7). This crest is thin anteroposteriorly, and probably could not have served any combative purpose (Hammer, 1997). There are raised ridges along the anterior and posterior sides of the crest, giving it a furrowed appearance.

Several small pits are present in a small depression in the angle between the ventral and rostral rami on the lateral side of the right lacrimal. It is unclear how far these small pits extend into the lacrimal, but this area does not appear to be extensively excavated. The largest depression is teardrop shaped in lateral view, with its long axis running anteroposteriorly, similar to the condition in *Eustreptospondylus* (Sadleir, 2004). This depression is located slightly more anteriorly than is typical for the lacrimal fenestra, which is tucked into the posterodorsal corner of the lacrimal in most theropods (though see *Zupaysaurus* PULR-076, Arcucci & Coria, 2003; and *Eustreptospondylus*, Sadleir, 2004). Abelisaurids are also unique in possessing lacrimal fenestrae that are displaced medially and are not visible in lateral view (O. Rauhut, pers. comm. 2006).

As in other theropods, a rounded and rugose process is present on the lateral part of the lacrimal, near the posterodorsal portion of the antorbital fenestra (Fig. 4). Currie & Zhao (1994a: 2045) suggested that this process demarcates the anteroventral extent of the eyeball and was for attachment of Ligamentum suborbitale. This ligament extends from the lacrimal to the postorbital and participates in the formation of the ventrolateral wall of the orbit in modern birds (Baumel & Raikow, 1993). The Ligamentum suborbitale process is located rather high on the lacrimal relative to the orbit, such that the eye would be restricted to a small portion of the dorsal part of the orbit if the suborbital ligament attached there, as was the case for at least some specimens of *Allosaurus* (Chure, 1998). This process is similar in morphology to that of *Sinraptor*, *Allosaurus* and *Yangchuanosaurus*, and does not extend as far posteriorly into the orbit as in abelisaurids and *Acrocanthosaurus*. The rounded posterolateral rim of the lacrimal extends posteroventrally and slightly laterally from the ventral portion of this process. The lacrimal is thinnest anteroposteriorly immediately ventral to this process, partially due to 'twisting' of the lacrimal body here. A distinct lacrimal antorbital fossa is developed on the descending ramus of the lacrimal (Fig. 4).

The sublacrimal portion and anterior process of the right jugal is preserved, although its dorsal contact with the lacrimal is partially obscured by white plaster. The postorbital process of the left jugal has been broken off from the main jugal body, and is preserved in articulation with the left postorbital. Neither jugal
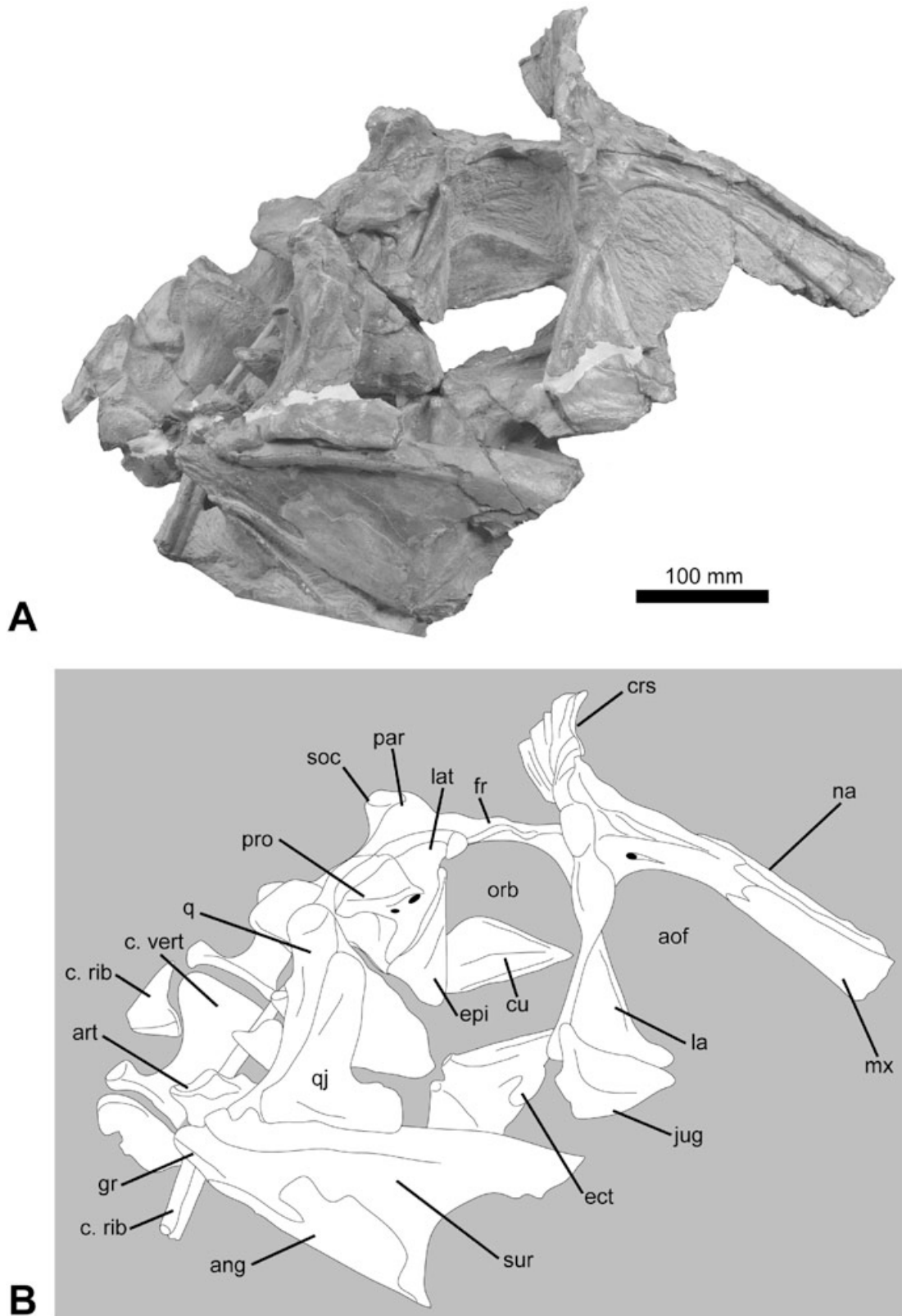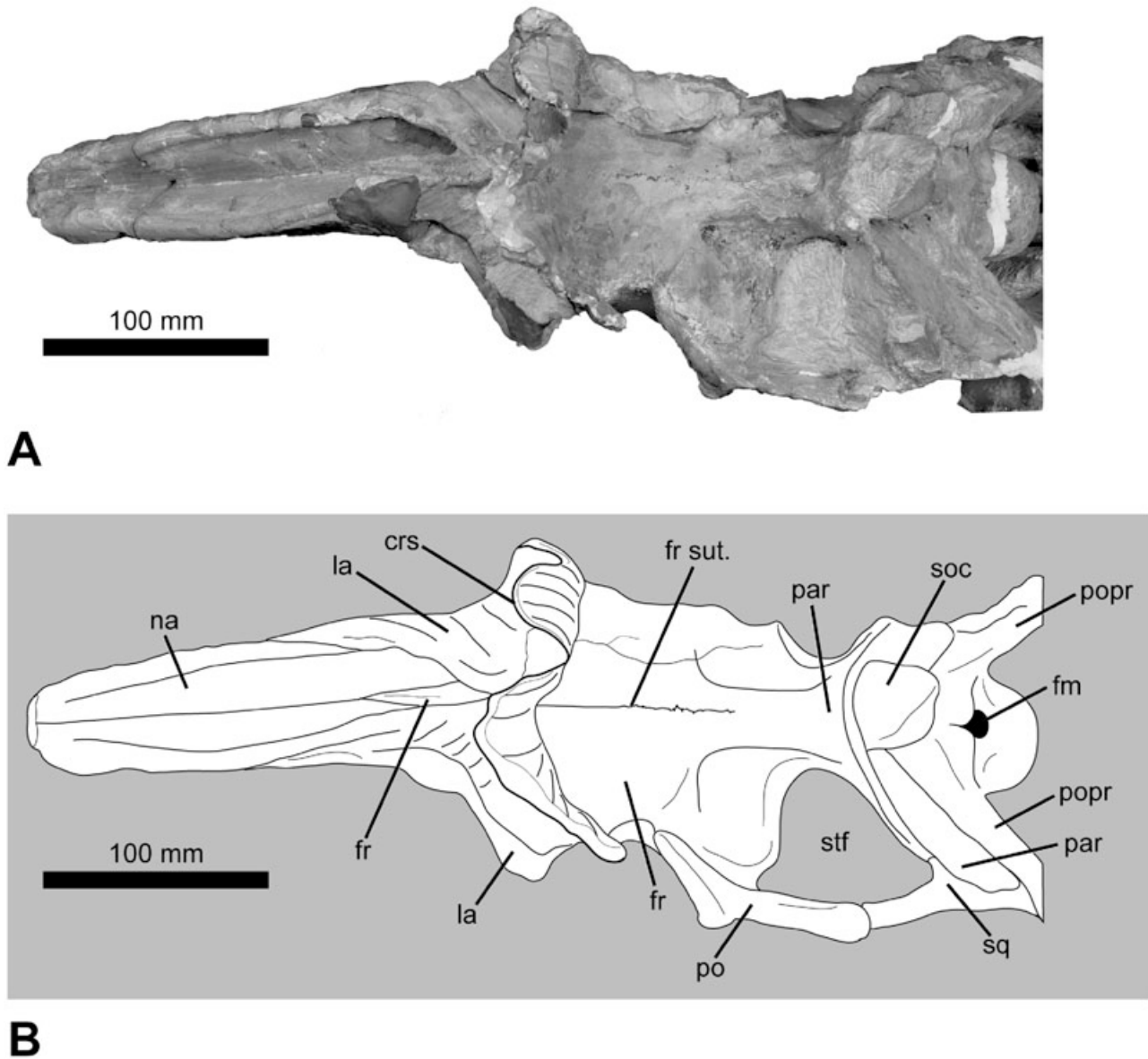
Figure 4. Skull of *Cryolophosaurus ellioti* in right lateral aspect (A), and interpretive line drawing (B). Several articulated posterior cervical vertebrae are preserved on the same block, posterior to the skull, and are visible in ventral aspect (photo courtesy of J. Weinstein).
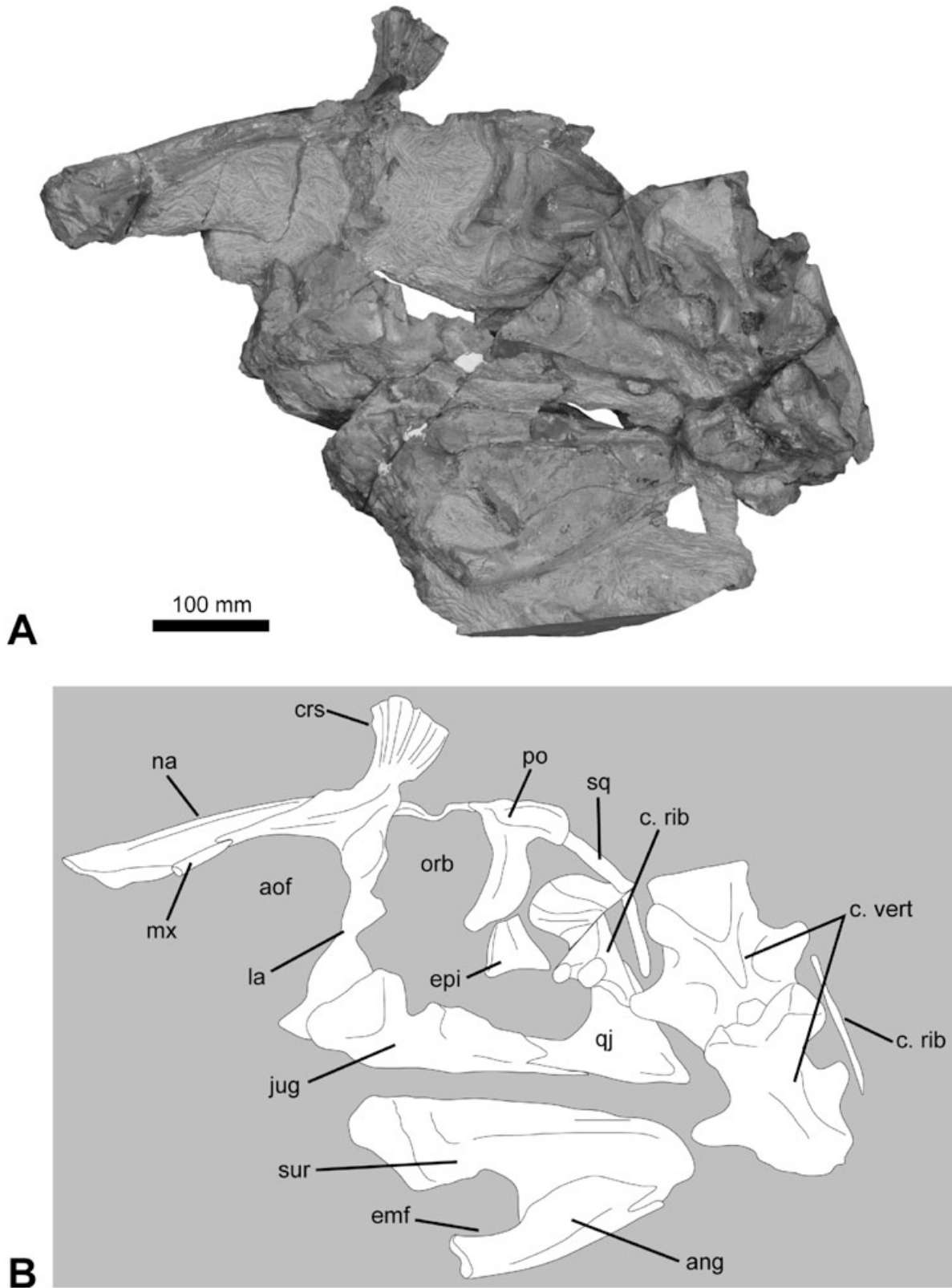
Figure 5. Skull of *Cryolophosaurus ellioti* in left lateral aspect (A), and interpretive line drawing (B). Several articulated posterior cervical vertebrae are preserved on the same block, posterior to the skull, and are visible in dorsal aspect (photo courtesy of J. Weinstein).
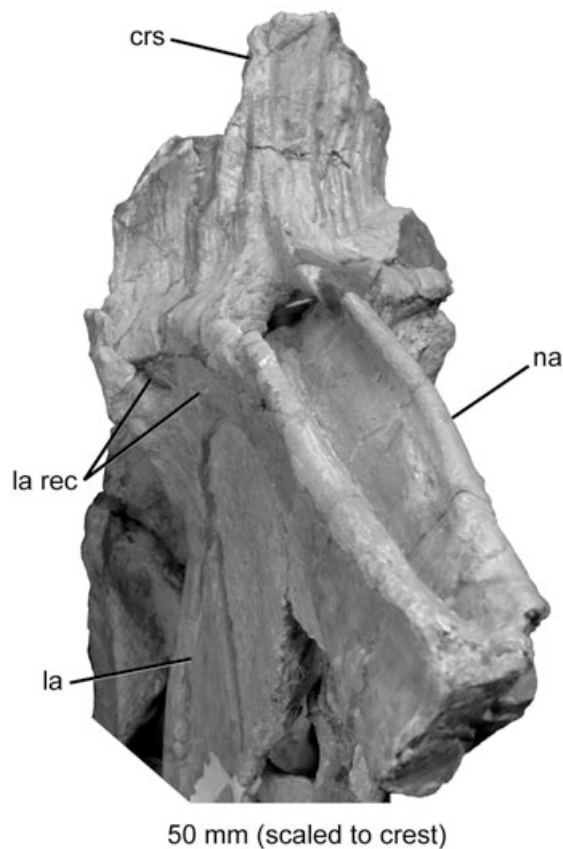
Figure 6. Skull of *Cryolophosaurus ellioti* in dorsal aspect (photo courtesy of J. Weinstein).

preserves a complete quadratojugal process, though the left jugal preserves most of the base of this process.

The anterior end of the jugal is clearly expanded as in most tetanuran theropods and *Dilophosaurus wetherilli* (UCMP 37302), but it is difficult to determine whether it participates in the internal antorbital fenestra. Thus, it is unclear whether the anterior process of the jugal completely separates the maxilla from the lacrimal externally. However, if the maxilla and lacrimal did have a contact, it would only be slight, and confined to the anteroventralmost corner of the
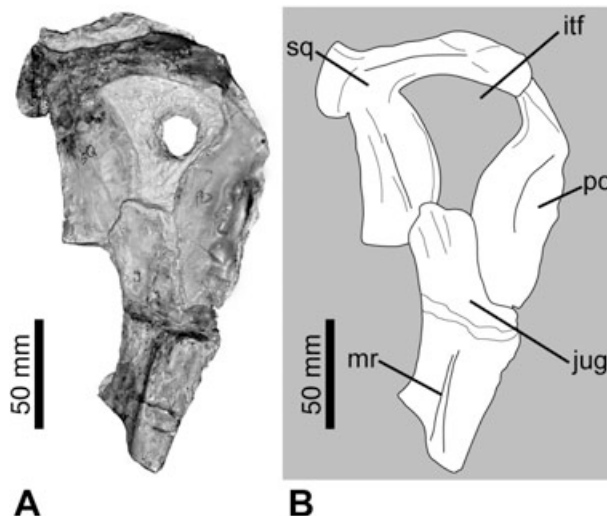
lacrimal. The relationship between the jugal, lacrimal and maxilla in the posteroventral corner of the antorbital fossa is similar to that present in *Dilophosaurus wetherilli* (UCMP 37302). Just posterior to the expanded anterior process, the jugal is pinched dorsoventrally where it forms the ventral border of the keyhole-shaped orbit. This portion of the jugal is better preserved on the left element, which shows a distinct V-shaped orbital margin (Fig. 5). The antorbital fossa extends onto the anterior process of the jugal, giving the expanded process a smooth, concave lateral surface. The jugal antorbital fossa is bounded by a low,

Figure 7. Skull of *Cryolophosaurus ellioti* in anterior, and slightly oblique anterior aspect, highlighting the ornamentation of the dorsal crest (photo courtesy of J. Weinstein).

Figure 8. Portions of the left jugal, postorbital and squamosal of *Cryolophosaurus ellioti* in medial aspect (A), and interpretive line drawing (B). These elements have been split in half from the left side of the skull.

crescent-shaped rim in its posterolateral corner, as in most tetanurans. No pneumatic foramina are present within the jugal antorbital fossa.

The postorbital process projects from the dorsal edge of the main body of the jugal and its base is subcircular in cross-section. The postorbital process of the jugal is tall and thickened anteroposteriorly, in contrast to the relatively slender morphology present in most theropods (Fig. 8). A thickened longitudinal ridge extends across the medial side of the postorbital process of the jugal, as in *Allosaurus* (AMNH FR600) and *Sinraptor* (Currie & Zhao, 1994a). In *Dubreuillosaurus* (MNHN 1998-13) and *Torvosaurus* (Britt, 1991) this medial ridge is not well developed. The postorbital process has a distinct curvature in lateral view, such that its anterior and posterior borders are convex and concave, respectively (Fig. 8). The posterolateral part of the tip of the postorbital process is situated adjacent to the anteromedial tip of the ventral ramus of the squamosal. This creates a unique constriction across the infratemporal fenestra, which is shaped like a figure-8.

Only the proximodorsal end of the quadratojugal process of the left jugal is preserved (Fig. 5). It is tallest at its base, and tapers posteriorly from the main body of the jugal and the posterior base of the postorbital process. The infratemporal fenestra extends anteroventrally onto the posterodorsal portion of the jugal as a distinct fossa. The angle formed by anterior and ventral margins of the infratemporal fenestra is slightly larger than 90 . The base of the quadratojugal process is depressed medially along this fossa.

The right prefrontal is preserved in contact with the bones of the skull roof and orbit. It is well developed and forms the anterodorsal rim of the orbit. This condition is similar to that present in many basal theropods, including the Mid-Jurassic tetanuran *Monolophosaurus* (Zhao & Currie, 1994). The prefrontal articulates with the anterolateral side of the frontal, just posterior to the base of the extended lacrimal crest, though the exact suture between the two elements cannot be traced. The prefrontal extends further laterally above the orbit than the frontal. Its posteroventral border is smooth and curved along the orbital margin.

Both frontals are preserved in contact with each other and are relatively complete (Fig. 6). The dorsal surfaces of the frontals are also not well preserved, making it difficult to identify sutures, with the exception of the interfrontal suture. The frontal is relatively flat and unornamented. It is considerably longer than wide, and does not contribute to the distinct midline crest. The interfrontal suture is straight anteriorly, but sinuous posteriorly (Fig. 6), similar to the condition described in *Dubreuillosaurus valesdunensis*

(Allain, 2002: 551). Anteriorly, the frontals narrow considerably to form a triangular process separating the nasals on the midline posteriorly. The tapered anterior end of each frontal is even more attenuated than in other theropods that have anteriorly triangular frontals, such as '*Syntarsus*' *kayentakatae* (Tykoski, 1998: fig. 6).

The supratemporal fossa extends anteriorly onto the dorsal surface of the posterolateral portion of the frontal. This portion of the supratemporal fossa is deepest at its anteromedial corner, creating a rounded, 90 arced rim in the posterolateral part of the frontal. The posterolateral wing of the frontal contacts the anterolateral portion of the parietal in the ventral part of this fossa, but the suture between the elements is difficult to determine. The frontoparietal suture about the midline is also not clearly preserved on the dorsal surface of the skull, but it is apparent from the sinuous midline suture of the frontals that the frontoparietal suture is located at least several centimetres posterior to the level of the anterior emargination of the supratemporal fossa. Lateral to the anterior extension of the supratemporal fossa the frontal articulates with the postorbital. This articulation is along an angle, such that anteriorly it is closer to the midline, and the posterior portion of the articulation is situated more laterally. The dorsal surface of the postorbital rises slightly higher than the lateral portion of the frontal along their articulation. The frontal is emarginated slightly medially anterior to its contact with the postorbital. The lateral surface of the frontal is smooth and slightly rounded here, where it contributes to the dorsal portion of the orbital rim. The frontals are weakly concave ventrally along their contribution to the orbital rim.

Both parietals are preserved in contact with the rest of the elements of the skull. They are almost entirely complete, although their surfaces are worn and damaged. At the frontoparietal suture the parietal is expanded slightly laterally, as is typical for most theropods (Currie & Zhao, 1994a: 2045). The dorsal surface of the parietal is relatively flat, with a lateral emargination from the supratemporal fossa. The parietal is expanded laterally at its anterior and posterior edges, such that it is laterally concave along the supratemporal fossa. Posteriorly, a midline process of the parietal contacts the anterodorsal surface of the supraoccipital wedge. The parietal does not extend much higher dorsally than the supraoccipital, as in most basal theropods (Currie & Zhao, 1994a: 2046). Lateral to the posterior midline process the parietal expands posterolaterally and ventrally into a large occipital wing (*sensu* Sues *et al.*, 2002: 540). The occipital wing of the parietal is thin anteroposteriorly compared with the rest of the parietal, and is concave posteromedially. The posterior border of the supratemporal fossa extends onto the anterior border of the occipital wing. Posteroventrally, the occipital wing comes to rest on the anterodorsal surface of the paroccipital process of the exoccipital. Dorsolaterally and laterally, the occipital wing contacts the squamosal, but only a small portion of this articulation is preserved at the anterodorsal tip of the left occipital wing.

The right postorbital is missing, and the left element is preserved in two parts. The medial side is still articulated with the majority of the skull, while the lateral half is broken off and preserved in contact with the postorbital process of the left jugal and the left squamosal (Fig. 8). The postorbital is roughly T-shaped in lateral view, with its long axis running dorsoventrally. In cross-section, the ventral process of the postorbital is roughly subcircular or triangular. The ventral process of the postorbital is distinctly curved, such that its anterior border is slightly concave, and its posterior border is convex. A suborbital flange is not present. The medial side of the dorsal portion of the postorbital articulates at an angle with the lateral projection of the frontal. Only the base of the squamosal process of the postorbital is preserved. It is thickest dorsoventrally at its base and extends posterodorsally from the posterodorsal portion of the main body of the postorbital. It articulates with a lateral groove in the intertemporal process (*sensu* Allain, 2002: 554) of the squamosal.

The majority of the left squamosal is preserved in two distinct portions, in a condition similar to that of the left postorbital. The medial portion of the squamosal is still articulated with the skull, while the lateral half is broken off and preserved in articulation with the left postorbital and the postorbital process of the left jugal (Fig. 8). The squamosal has an anteroposteriorly broad quadratojugal process extending ventrally to contact the quadratojugal. As mentioned above, the anteroventral corner of the quadratojugal process of the squamosal contacts the posterodorsal portion of the postorbital process of the jugal, dividing the infratemporal fenestra.

The intertemporal process is very long, and extends anteriorly from the anterodorsal corner of the body of the squamosal. This is similar to the condition present in *Dilophosaurus wetherilli* (UCMP 37302). The intertemporal process is thinnest dorsoventrally at its base, and expands slightly dorsoventrally at its contact with the intertemporal ramus (*sensu* Allain, 2002: 553) of the postorbital. The angle between the quadratojugal and intertemporal processes of the squamosal is less than 90 , in contrast to the wide angle present in the squamosals of most theropods (Allain, 2002), but very similar to the morphology present in *Dilophosaurus wetherilli* (UCMP 37302), and *Zupaysaurus* (Arcucci & Coria, 2003). A low, thin ridge appears to be present on the middle of the medial side of

the intertemporal process, running anteroposteriorly along its length. Only the lateralmost base of the paroccipital process of the left squamosal is preserved, projecting medially from the posterodorsal corner of the body of the squamosal.

The quadratojugal is roughly L-shaped in lateral view and forms most of the posterior and ventral margins of the infratemporal fenestra (Fig. 4). It is partially co-ossified to the lateral side of the quadrate, though traces of the suture between these two elements can be seen, particularly at their dorsal ends. The posterolateral corner of the quadratojugal is robust and knob-shaped. The quadratojugal possesses a tall and anteroposteriorly broad dorsal process. The dorsal tip of the process is not entirely preserved, though it would have contacted the squamosal just rostral to the quadrate cotyle. The anterior process of the quadratojugal is transversely thin. It is thick dor-

soventrally at its base, and tapers anteriorly. A thin, splinter-like groove on the ventrolateral surface of the anterior process may represent the articulation for the ventral prong of the quadratojugal process of the jugal. The absence of a similar groove dorsal to this one for reception of the dorsal prong of the quadratojugal process suggests that the ventral prong of the quadratojugal process is longer than the dorsal prong, as in most theropods (Allain, 2002: 554; Tykoski, 2005).

The right quadrate is more visible than the left, which is partially obscured by two articulated cervical vertebrae (Fig. 9). A very small paraquadrate fenestra may be present on the posterolateral side of the quadrate, but a large crack in this area makes interpretation difficult. This foramen is oval-shaped and almost completely surrounded by the quadrate. The quadrate is tall and its single dorsal head is located approxi-
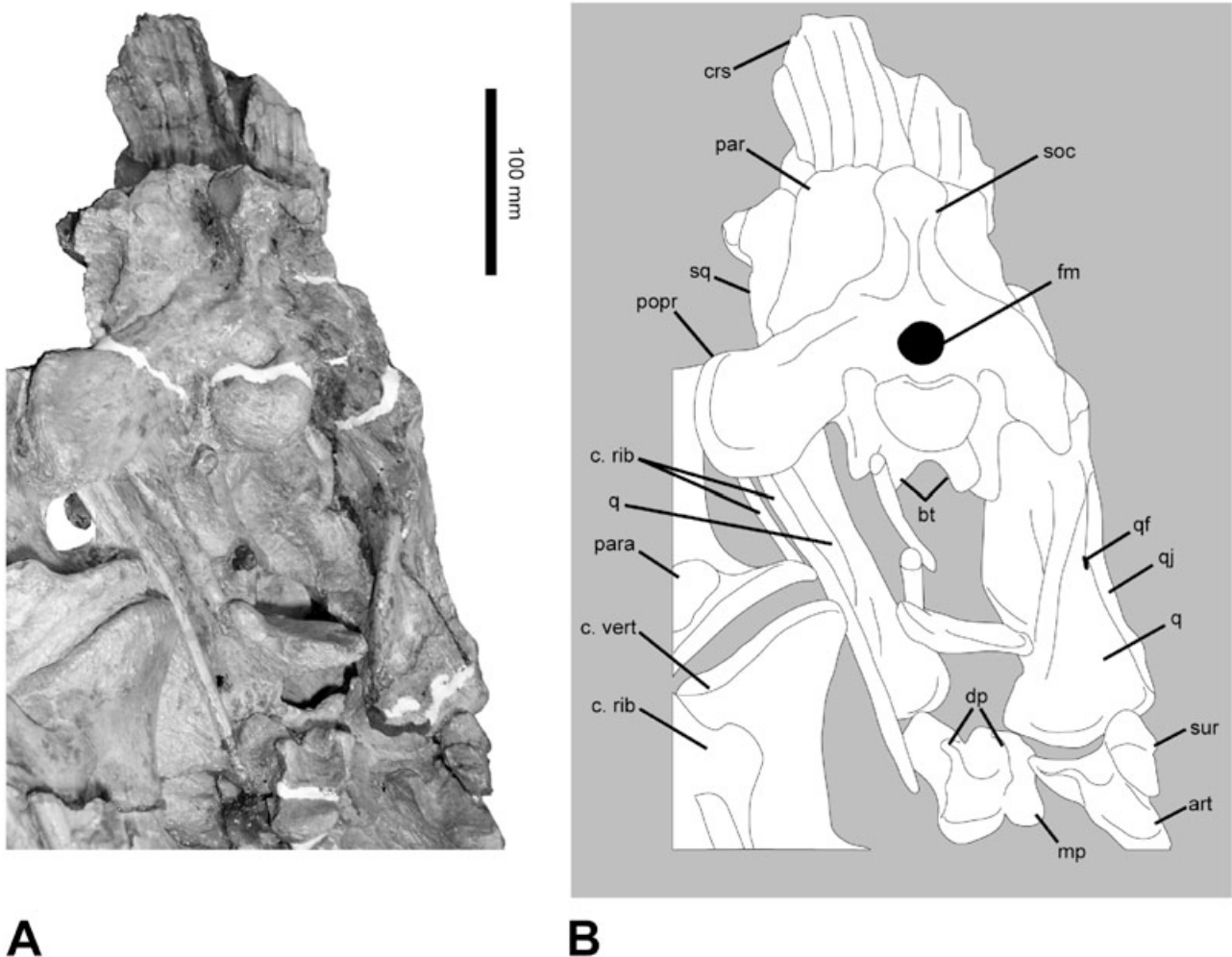
Figure 9. Skull of *Cryolophosaurus ellioti* in posterior aspect (A), and interpretive line drawing (B). Portions of two articulated posterior cervical vertebrae and ribs are visible in lateral aspect posterolateral to the skull.

mately level with the middle of the orbit. The distal articular end of the quadrate has distinct medial and lateral condyles, as in most theropods. The lateral condyle is wider mediolaterally than anteroposteriorly, while the long axis of the medial condyle runs approximately anteromedially to posterolaterally. A prominent rounded ridge arises from the posteromedial portion of the medial condyle and runs craniolaterally up the quadrate, as though the body of the quadrate is twisted 90 laterally about the jaw articulation. The left quadrate has been displaced anteriorly and slightly laterally, particularly at its dorsal end (Fig. 9). Part of this post-mortem crushing may contribute to the displacement of the left squamosal, and accentuates the constriction of the infratemporal fenestra between this element and the dorsal ramus of the left jugal.

The right ectopterygoid is preserved in slight disarticulation with the right pterygoid. Portions of the dorsal surface and jugal ramus are visible in the ventral margin of the orbit. The hooked jugal process is circular in cross-section, and extends from the anterolat-eral body of the ectopterygoid. It extends laterally at its base, and then curls posteriorly along its lateral contact with the jugal. The distal tip of the jugal process is not preserved.

The majority of the right epipterygoid is preserved in articulation with the antero-ventrolateral portion of the braincase (Fig. 10). The thin, ventralmost portion is missing, however. Part of the ventral portion of the left epipterygoid is also preserved in articulation. The dorsal half of the left epipterygoid is hidden beneath the ventral flange of the left postorbital. The epipterygoid is an elongate triangular element covering the ventrolateral side of the braincase. Its anterior edge is straight, while its posterior border is slightly concave. The epipterygoid has a broad ventral flange that articulates with the lateral surface of the quadrate process of the pterygoid. Here the epipterygoid faces anterolaterally, and it twists slightly laterally as it narrows dorsally. Dorsally, the narrow tip of the epipterygoid contacts the laterosphenoid. The anterior edge of the epipterygoid is rounded in cross-section, and thickened relative to the rest of the bone. This thickened
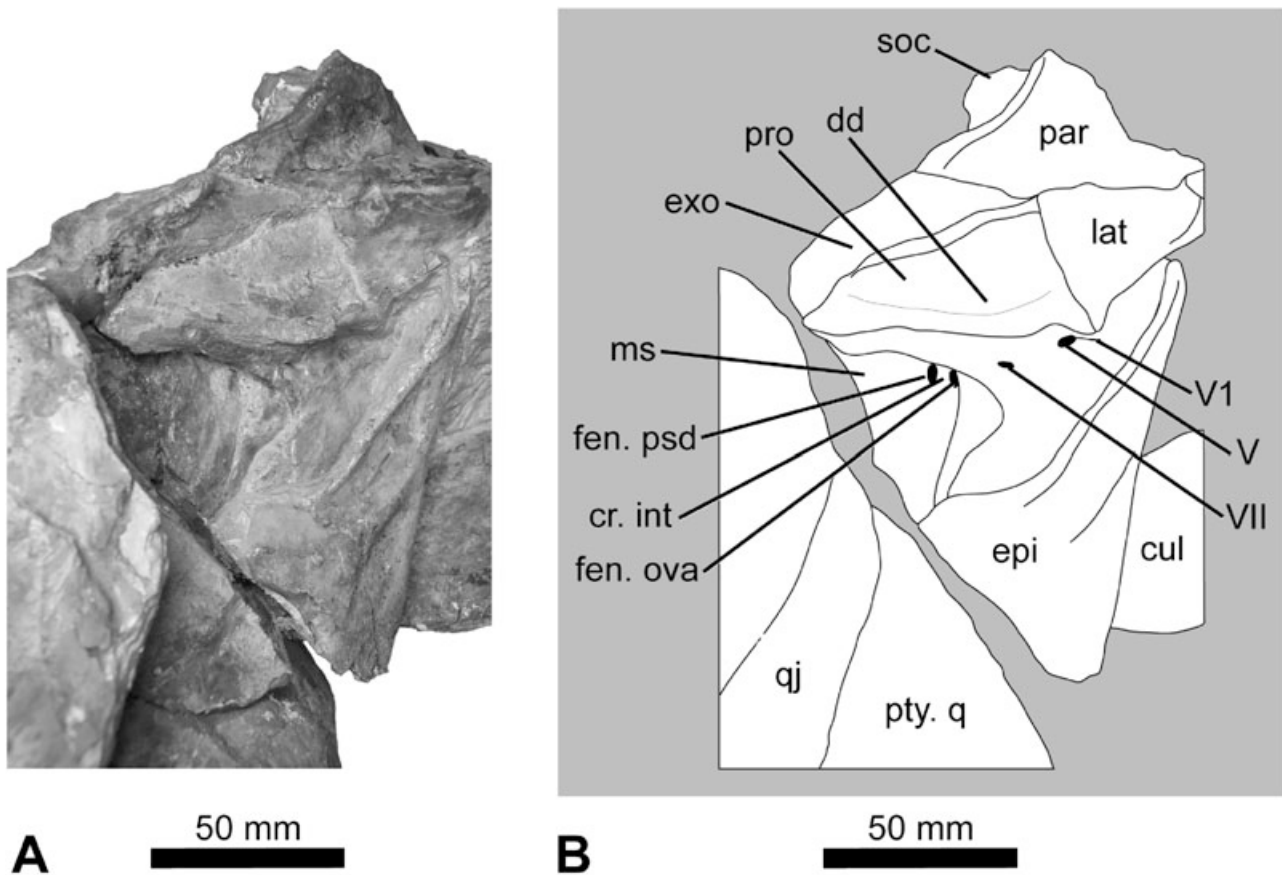
Figure 10. Braincase of *Cryolophosaurus ellioti* in right lateral aspect (A), and interpretive line drawing (B).

edge gives the epipterygoid much of its 'twisted' appearance along its long axis. There are two additional ridges on the epipterygoid that are also rounded and slightly thickened. One runs up the posterior border of the bone, meeting the anterior ridge dorsally as the epipterygoid narrows to a point. The dorsal tip of the epipterygoid extends slightly laterally here. The other ridge runs parallel to this one, but is located on the middle of the lateral face of the epipterygoid, and thus is shorter and intersects the anterior ridge near its middle. This middle ridge is not quite as well developed as those of the anterior and posterior border of the epipterygoid, and it blends smoothly into the ventral border of the bone. Together, the three ridges create two shallow, triangular concavities on the lateral surface of the epipterygoid.

Sutures between elements of the posterior braincase are difficult to make out due to fusion, as well as the overall preservation of the material. The spherical occipital condyle is formed mainly by the basioccipital, with small contributions from the exoccipitals forming its dorsolateral borders (Fig. 9). The articular surface of the occipital condyle is rounded and rugose, and is separated from the main body of the basioccipital by a distinct neck. There is a faint line running around the base of the occipital condyle, separating the smoother bone of the neck from the more rugose articular surface. The neck of the occipital condyle is short and stout, as in *Piatnitzkysaurus* (PVL 4073), and is not significantly constricted. The dorsal portion of the occipital condyle is damaged along its neck, and has been partially repaired with white plaster. In most theropods the hypoglossal nerve (CN XII) exits through a foramen in the anterolateral base of the occipital condyle at its constricted neck, but this region is obscured by the crack. A broad, shallow medullar groove extends across the dorsal surface of the occipital condyle to its articular end. This groove, coupled with the contributions of the exoccipitals to the dorsolateral corners of the occipital condyle, give the condyle a kidney-shaped appearance in posterior aspect. As in most non-coelurosaurian theropods, the occipital condyle is larger than the foramen magnum (Rauhut, 2004: 1110).

The foramen magnum is subcircular in outline, and only slightly broader than high. Due to the repaired portion of the neck of the occipital condyle, it is unclear whether the dorsal portion of the basioccipital made a small contribution to the floor of the foramen magnum, as in some basal tetanurans (Allain, 2002: 555). The majority of the border of the foramen magnum is formed by the ventrolateral extensions of the exoccipitals, which curl around the ventrolateral borders of the foramen magnum, extending onto the dorsolateral corners of the occipital condyle, and also curl dorsomedially around the foramen magnum to form

its lateral and dorsal borders. The dorsomedial extensions of the exoccipitals exclude the ventral portion of the supraoccipital from participation in the dorsal border of the foramen magnum. This condition is similar to that seen in *Dilophosaurus wetherilli* (Welles, 1984), '*Syntarsus*' *kayentakatae* (Tykoski, 1998), *Coelophysis rhodesiensis* (Raath, 1977), *Coelophysis bauri* (Colbert, 1989), *Piveteausaurus* (Allain, 2002; *contra* Taquet & Welles, 1977), *Acrocanthosaurus* (Stovall & Langston, 1950), and at least some specimens of *Allosaurus* (Madsen, 1976; AMNH FR 600). A small, shallow, vertically orientated furrow is located on the midline of the dorsal border of the foramen magnum, where the dorsomedial extensions of the exoccipitals meet.

Ventral to the base of the occipital condyle, the basioccipital forms the posterior portions of the basal tubera. The basal tubera are separated from each other by a distinct median notch, unlike the condition in *Allosaurus* (Madsen, 1976) and *Sinraptor* (Currie & Zhao, 1994a). This notch is narrow and weakly V-shaped, but is not similar to the morphology present in most troodontids, where the basal tubera are extremely reduced and separated by a narrow, V-shaped notch (Makovicky *et al.*, 2003). The basal tubera are robust but relatively short, extending ventrally and slightly laterally from the base of the occipital condyle. The basal tubera are much shorter than in most theropods, and resemble the abbreviated basal tubera of '*Syntarsus*' *kayentakatae* (Tykoski, 1998: fig. 9). They are slightly expanded mediolaterally, and rounded at their ventral tips. The distance across the basal tubera is greater than the transverse width of the occipital condyle.

The supraoccipital is a massive, triangular bone on the posterodorsal side of the braincase (Fig. 9). It is extensively fused with the exoccipitals along its ventrolateral margins. A conspicuous midline ridge (= 'nuchal crest' of Sues *et al.*, 2002) is present on the posterior side of the supraoccipital. It begins just dorsal to the contact between the exoccipitals over the foramen magnum, and extends dorsally several centimetres before expanding mediolaterally into a large, triangular supraoccipital wedge (*sensu* Zhao & Currie, 1994: 2031). The midline ridge is thin mediolaterally and triangular in transverse section. The posterior border of the ridge is slightly rounded and rugose, and its lateral borders probably served as the point of attachment for the ligamentum nuchae (Sues *et al.*, 2002: 542).

A pair of shallow, rounded depressions are present on either side of the midline ridge, separating the lateral wings of the supraoccipital from its dorsal process. Due to the lack of clear sutures between the supraoccipital and the exoccipitals, it is not clear whether these depressions are confined to the lateral

sides of the supraoccipital [as suggested by Zhao & Currie (1994: 2031), and Sues *et al*. (2002: 542) for *Monolophosaurus* and *Irritator*, respectively], or extended onto the dorsomedial portions of the exoccipitals [as interpreted by Raath (1977, 1985) and Tykoski (1998: 44) for *Coelophysis rhodesiensis* and '*Syntarsus*' *kayentakatae*, respectively]. Regardless of the exact margins of these bowl-shaped depressions, they probably served as insertion points of M. rectus capitis (Raath, 1977; Tykoski, 1998: 44; Sues *et al*., 2002: 542). In most theropods, the external occipital vein (V. cerebralis media, or V. occipitalis externa) typically exits the skull from within this depression as well (Currie & Zhao, 1994a; Sues *et al*., 2002; Currie, 2003), though this opening is not preserved in *Cryolophosaurus*.

The supraoccipital wedge is slightly wider mediolaterally than the width of the foramen magnum, though not as robust as the supraoccipital wedges of *Carcharodontosaurus*, *Giganotosaurus* and *Sinraptor* (Coria & Currie, 2002). It has an inverted triangular shape in posterior aspect, and is approximately square in dorsal view. Its anterior edge contacts the concave midline surface of the articulated parietals. A short midline process of the articulated parietals laps slightly over the anterodorsal surface of the supraoccipital. This may be homologous to the tongue-like posterior process of the parietals that articulates with the supraoccipital wedge in large theropods such as *Abelisaurus*, *Carnotaurus*, *Majungatholus*, *Sinraptor*, *Acrocanthosaurus*, *Allosaurus* and *Giganotosaurus* (Coria & Currie, 2002: 805, character 14; Madsen, 1976: fig. 11, AMNH FR 600). The preserved surface of the supraoccipital wedge is globular and rugose.

The exoccipital and opisthotic are indistinguishably fused together into a single element ('otoccipital' of Sues *et al*., 2002: 542). In dinosaurs these elements fuse prior to maximum size during ontogeny, though the relative timing of this ossification is poorly known (Currie, 1997; Tykoski, 1998: 42). Welles (1984) and Charig & Milner (1997) reported unfused exoccipitals and opisthotics in the theropods *Dilophosaurus wetherilli* and *Baryonyx*, but both of these taxa are known from subadult specimens (Tykoski, 1998: 42). The exoccipitals form the lateral and dorsal borders of the foramen magnum (Fig. 9). They contact each other above the foramen magnum, and are separated from each other by the basioccipital below the foramen magnum. A distinct depressed area is present on either side of the base of the occipital condyle, between the condylar portion of the exoccipital and the base of the paroccipital process. This depression (= 'paracondylar pocket' of Tykoski, 1998) has a semicircular dorsal rim, and is better preserved on the left side. The rim of the paracondylar pocket is most distinct along its dorsomedial edge. Branches of the hypo-

glossal nerve (XII) exit from small foramina within the medial portion of this pocket in all theropod dinosaurs. In many theropods, a larger foramen, the vagus foramen, is also present in the anterolateral portion of the paracondylar pocket, marking the exit of the jugular vein, and the vagus (X) and accessory (XI) nerves (Allain, 2002; Rauhut, 2004; Sanders & Smith, 2005). These foramina are not visible in *Cryolophosaurus*, either because they are not present in this area and may have instead exited the braincase laterally, or more likely because they are still obscured by several cracks and matrix that is present in the deepest part of the paracondylar pockets. The ventral orientation of the paroccipital processes may also aid in obscuring these foramina, as it appears to do in *Ceratosaurus* (Sanders & Smith, 2005).

Laterally, the exoccipitals make up the robust paroccipital processes. The left paroccipital process is more complete than the right. The anterodorsal side of the base of the paroccipital process is lapped by the occipital wing of the parietal (see Fig. 13). A small groove is present on the anterolateral base of the paroccipital process, slightly anterior and lateral to the stapedial groove. A broad, shallow fossa is present on the anterolateral face of the base of the paroccipital process, posterior to where its contact with the prootic would be. Similar fossae appear to be present in this location in *Ceratosaurus* (MWC 1; Sanders & Smith, 2005: fig. 1B), and *Allosaurus* (UUVP 5583; Madsen, 1976: fig. 15). A low, rounded ridge extends down the midline of the proximal half of the posterior side of the paroccipital process. This ridge begins from the portion of the exoccipital contributing to the dorsolateral border of the foramen magnum. The paroccipital processes are thinnest dorsoventrally at their base lateral to the paracondylar pockets, and they gradually thicken distally, becoming expanded and fan-shaped at their distal ends, as in most mid-sized to large theropods. The paroccipital processes are directed strongly posteriorly and also ventrally, such that the ventral margins of their distal ends extend beyond the level of the occipital condyle posteriorly and terminate slightly below the level of the ventral portion of the basioccipital. This is similar to the condition in *Monolophosaurus*, *Sinraptor* and several other tetanurans. The processes do not extend as far ventrally as in *Allosaurus* and *Acrocanthosaurus*. The distal ends of the paroccipital processes are twisted slightly rostrally, such that their dorsal tips are slightly anterior to their ventral tips.

Both metotic struts (*sensu* Witmer, 1990; = 'crista metotica', 'crista tuberalis', 'ventral buttress' of other authors) are visible in posterior and lateral aspect. The anteroventral edge of the metotic strut begins as the posteroventral border of the stapedial groove, which runs along the ventral base of the paroccipital

process from fenestra ovalis. The stapedial groove provides the pathway for the columella (stapes) and its stapedial footplate to fenestra ovalis. This groove may have also transmitted the internal jugular vein from the braincase (Rauhut, 2004: 1118). The metotic strut runs anteroventrally from the base of the paroccipital process, passing the lateral side of the basal tuber to the lateral side of the basisphenoid, separating the lateral and posterior walls of the braincase, as in most theropods with the exception of carcharodontosaurids (Coria & Currie, 2002). In posterior aspect the metotic strut does not extend significantly further ventrally than the basal tuber, as in *Sinraptor* (Currie & Zhao, 1994a: 2049). The anterolateral side of the metotic strut forms the posteromedial wall of the otic region. Two small foramina are located at the anterior base of the paroccipital process, posteromedial to the opening for the facial nerve (CN VII) on the prootic. The anterior opening probably represents fenestra ovalis, into which the head of the stapes would have fit. The slightly larger, and more posterior, opening probably represents fenestra pseudorotunda. This opening may have transmitted the ninth cranial nerve (CN IX), as in other theropods (Currie & Zhao, 1994b; Rauhut, 2004;: 1117). There is a small bar of bone separating fenestra pseudorotunda and fenestra ovalis, which is the interfenestral crest (= 'crista interfenestralis'). Currie & Zhao (1994b) claim that the interfenestral crest of *Troodon*, *Archaeopteryx*, *Protoavis* and all living archosaurs is formed by the opisthotic. However, Tykoski (1998: 42) notes that in '*Syntarsus*' *kayentakatae*, the interfenestral crest appears to be derived from either the prootic or the basisphenoid. This may account for the slightly different morphology of the interfenestral crest, and arrangement of the fenestra ovalis and fenestra pseudorotunda in this taxon (see Tykoski, 1998: fig. 10). In *Cryolophosaurus*, the interfenestral crest appears to be entirely composed of the opisthotic portion of the fused exoccipital-opisthotic.

The prootic forms the majority of the lateral wall of the braincase, and is broadly visible on the right side of the skull (Fig. 10). The posterior portion of the prootic laps over the anterior side of the base of the paroccipital process. The ventral border of this posterior process forms the overhanging dorsal border of the otic region. The anterior border of the otic region is formed by a ventral projection of the prootic, which extends onto the basisphenoid. The dorsal half of the prootic overhangs the ventral portion of the braincase laterally. The prootic is slightly thickened and rugose at the lateral edge of this shelf. There is a shallow, triangular depression on the dorsal surface of the prootic, as in most theropods (Rauhut, 2004: 1114). This depression is probably the homologue of the dorsal tympanic recess (*sensu* Witmer, 1997: 156), which

is present in all known birds. However, as noted by Norell, Makovicky & Clark (2000: 9), the homology of this depression and the avian dorsal tympanic recess has not been established with certainty. The lack of pneumatic foramina associated with this depression in *Cryolophosaurus* also limits the ability to identify it as a pneumatic feature. The possibility that this depression may have served as a site of attachment for deep jaw muscles, as suggested by several authors (Raath, 1985; Walker, 1985), cannot be ruled out either (Rauhut, 2004: 1120).

The trigeminal foramen is located just below the lateral shelf formed by the dorsal half of the prootic, ventral to the anterodorsal border of the prootic at its sutural contact with the laterosphenoid. The trigeminal foramen is small and oval, with its long axis running anterodorsal–posteroventral. The foramen opens anterodorsally, and there is a groove at its anterodorsal margin that extends anterodorsally across the laterosphenoid toward the posterodorsal part of the orbit. This sulcus probably carried the ophthalmic branch of the trigeminal nerve (V1), and may suggest that the three branches of the trigeminal nerve exited the braincase together through a single common opening (Sues *et al.*, 2002: 542).

The foramen for passage of the facial nerve is located posterior, and slightly ventral, to the trigeminal foramen, and just anterior to the anterodorsal border of the fenestra ovalis. Like the trigeminal foramen, the opening for CN VII is located below the lateral shelf formed by the dorsal half of the prootic. The opening for CN VII is small and slightly oval-shaped, with its long axis running anteroposteriorly. The foramen for CN VII opens lateroventrally as in *Piatnitzkysaurus* (PVL 4073).

The term crista prootica (= 'preotic pendant' of Welles, 1984; 'ala basisphenoidalis' of Chure & Madsen, 1998; 'rostroventral wing of prootic' of Elzanowski & Wellnhofer, 1996) is restricted here to the posteroventral process of the prootic, which is often hook-like in appearance in many tetanurans and neoceratosaurs. In *Cryolophosaurus*, the anteroventral portion of this structure is lapped over by the base of the epipterygoid. From what is visible, the crista prootica does appear to have a hook-like morphology, although the area posterior to it on the basisphenoid does not appear to be extensively excavated by an anterior tympanic recess, as in *Piatnitzkysaurus* (PVL 4073; Rauhut, 2004) and most tetanurans.

The laterosphenoid forms the anterolateral wall of the braincase, anterior, and slightly dorsal, to the prootic (Fig. 10). From its contact with the prootic, the laterosphenoid extends anterodorsally and laterally. A portion of the suture between the laterosphenoid and prootic is visible on the right side, just dorsal to the trigeminal foramen. Both the prootic and the lat-

erosphenoid are thickened at their contact along the lateral shelf overhanging the trigeminal foramen. The suture between the prootic and laterosphenoid extends posterodorsally from the lateral shelf overhanging the trigeminal foramen, across the lateral wall of the braincase. Just dorsal to this lateral shelf, the possible homologue of the dorsal tympanic recess extends onto the dorsolateral portion of the laterosphenoid as a shallow depression. Ventral to the thin lateral shelf of the braincase much of the right laterosphenoid is obscured by matrix and the dorsal flange of the epipterygoid. The anterodorsal projection of the laterosphenoid is not completely preserved, though it appears that it possessed a distally bifid condyle for its contact with the frontal and postorbital as in most theropods. Below the contact for the postorbital, the ventrolateral surface of the laterosphenoid contacts the thin dorsal process of the epipterygoid.

The parasphenoid is preserved in articulation with the other elements of the braincase, but only a portion of the cultriform process (= 'parasphenoid rostrum') is visible in the orbital region in right lateral view (Figs 4, 10). Matrix obscures its dorsal border and it is unclear if a longitudinal furrow is present along the dorsal margin. The cultriform process is plate-like and thin mediolaterally. It extends anteriorly, and slightly dorsally, from the basisphenoid, though its base is obscured by the ventral portion of the epipterygoid. The cultriform process has a distinct 'kink' in its dorsal border, giving the anteriormost portion of the process a triangular shape. A similar morphology is present in *Allosaurus* (UUVP 5961; Madsen, 1976). A less extreme bend in the dorsal border of the cultriform process is also present in *Dubreuillosaurus valesdunensis* (MNHN 1998-13; Allain, 2002).

Both right and left surangulars are preserved in articulation with the postdentary bones of the lower jaws (Figs 4, 5). They are both broken anterior to the external mandibular fenestrae. Both are massive elements, constituting the majority of the posterior mandibles. At their posterior tips they contact the articulars medially to form the mandibular glenoid. Ventrolaterally, the surangulars are overlapped by the broad, blade-like body of the angulars. The medial surfaces of the surangulars are not visible, except at their posteriormost ends, where they can be viewed on the large block from the same side as the posterior skull.

The posterior portion of the surangular is deeper dorsoventrally than the anterior portion, which thins towards its anterior articulation with the dentary. The lateral surface of the surangular is weakly convex. There is an extensive sutural surface for the posterior portion of the angular. The sutural surface for the angular is partially visible on the right surangular, where portions of the posterior blade of the angular

have been broken off. The surface is scarred and bears faint longitudinal striations, running parallel to the long axis of the posterior blade of the angular. As in most theropods, the dorsal surface of the surangular is thickened medially and folds over to form the dorsal roof of the adductor fossa (Currie & Zhao, 1994a: 2054). Anterior to the end of the lateral surangular shelf the dorsal surface of the surangular has a shallow, anteroposteriorly elongate depression for the insertion of M. adductor mandibulae externus (Currie & Zhao, 1994a: 2054). This depression is better preserved on the right surangular. The dorsal portion of the surangular is also thickest mediolaterally along the insertion of M. adductor mandibulae externus.

One of the most distinctive features of the surangular is the robust lateral shelf, which runs anteroposteriorly near the dorsal border of the surangular (Fig. 4). The shelf is thick and rounded, and runs anteriorly from the lateral side of the mandibular glenoid to just ventral of the depression for M. adductor mandibulae externus on the dorsal surface of the surangular. A small, posterodorsally opening surangular foramen is located under the posterior part of the lateral surangular shelf. The shelf is consistent in dorsoventral and mediolateral thickness throughout its length, and is not pendant anteriorly as in theropods such as *Allosaurus* (YPM 14554) and *Sinraptor* (Currie & Zhao, 1994a: fig. 11E). It is similar in morphology to the lateral surangular shelf of *Dilophosaurus wetherilli* (UCMP 37302), and '*Syntarsus*' *kayentakatae* (Tykoski, 1998), but thicker and more robust. Gauthier (1986: 10) suggested that the robust lateral surangular shelf in carnosaurs (*sensu* Gauthier, 1986) was associated with the insertion of enlarged pterygoideus musculature. However, no features on the shelf suggest that it served as a site of muscle insertion, particularly of M. pterygoideus, which inserts primarily on the medial side of the posterior jaw in extant birds (Vanden Berge & Zweers, 1993: 202). Tykoski (1998: 52) instead suggested that the lateral surangular shelf formed an extensive contact zone with the lower infratemporal bar during adduction of the lower jaws, and acted to brace the posterior jaw against lateral strain.

Posteroventral to the lateral surangular shelf, an oblique groove extends across the lateral side of the surangular, just anterior to the articulation with the caudal splint of the angular. A similar well-excavated groove is present on the lateral surface of the surangular of *Dilophosaurus wetherilli* (UCMP 37302). This groove extends to the end of the surangular in both taxa, and does not appear to represent an articular surface, as the caudal splint of the angular articulates with the surangular ventral to this groove.

Posteriorly, the lateral surangular shelf curves slightly medially and its posterodorsal end expands

dorsoventrally into the cup-shaped lateral mandibular glenoid. The lateral glenoid is narrow anteroposteriorly, which would have restricted fore–aft sliding movements of the lower jaw. The lateral glenoid fossa has a distinct U-shape in lateral aspect, and is much more enclosed than the condition in basal theropods such as '*Syntarsus*' *kayentakatae* (Tykoski, 1998), *Coelophysis bauri* (Colbert, 1989) and *Dilophosaurus wetherilli* (UCMP 37302), as well as the more distantly related *Herrerasaurus* (PVSJ 407), where there is little or no anterior wall to the lateral glenoid. A more confined, U-shaped lateral glenoid fossa is present in many neoceratosaurs and basal tetanurans, as well as *Zupaysaurus* (Ezcurra & Novas, 2007). A small lateral swelling is located immediately lateral to the lateral glenoid fossa and its anterior wall. This swelling may be homologous to the laterally projecting 'knob' present on the lateral glenoid of *Acrocanthosaurus* (Harris, 1998: 11). The anterior wall of the lateral glenoid rises at a right angle from the posterior part of the lateral surangular shelf. It is narrower anteroposteriorly than the posterior wall of the lateral glenoid, which rises at a gentler curve from the posterior portion of the lateral surangular shelf. The dorsal surface of the posterior wall of the lateral glenoid is flat and slopes gently posteroventrally, such that its flat surface faces posterodorsally. The anterior wall of the lateral glenoid rises to a short, rounded point at its midline, while the posterior wall is more level across its tip. There is no distinct 'spine' arising from the posterior wall of the lateral glenoid as in *Acrocanthosaurus* (Harris, 1998: 11).

The lateral glenoid part of the surangular contacts the lateral side of the articular, which curls around the ventromedial and posteroventral surfaces of the lateral glenoid. The rostral end of the articular is braced by a short, medial process extending from the dorsomedial border of the surangular. The articulation of the lateral glenoid and medial glenoid on the articular creates a small crest that runs anteroposteriorly across the middle of the entire, articulated glenoid. This ridge articulates with the groove between the quadrate condyles, and restricts mediolateral motion at the craniomandibular joint (Harris, 1998: 67). This interglenoid ridge (*sensu* Currie & Carpenter, 2000: 220) is characteristic of most theropods, with the exception of *Acrocanthosaurus*, where it is reduced (Harris, 1998: 11–12). The lateral glenoid fossa is situated slightly higher dorsally than the medial glenoid fossa on the articular, matching the uneven ventral border of the quadrate condyles.

Both right and left angulars are preserved in articulation with the postdentary bones of the lower jaws (Figs 4, 5). In general the left angular is the better preserved of the two. The anteriormost portions of both angulars are missing, and portions of the thin, fragile, dorsal blade of the posterior part of the right angular are broken as well. The angular forms the lateral wall of the ventral half of the posterior mandibles. It is a weakly curved plate of bone, with a dorsoventrally expanded posterior end and a thickened ventral margin. Anteriorly, the angular would have contacted the posterior part of the dentary medially, and the splenial laterally. The middle of the angular is the thinnest portion of the bone dorsoventrally, and its dorsal surface formed the ventral margin of the external mandibular fenestra. The dorsal surface of the angular along the external mandibular fenestra is weakly concave, and smooth with a gently rounded surface. Although only the ventral border of the external mandibular fenestra is preserved, it is clear that the fenestra was long anteroposteriorly, and was probably fairly large, as in most basal theropods. No distinct rugosities appear to be present on the lateral surface of the angular, as have been described for some theropods (Brochu, 2002: 48).

Posteriorly, the angular expands dorsoventrally into a blade-like process that overlaps the ventral half of the lateral face of the surangular. The ventral portion of this expanded posterior blade is much thicker than the thin dorsal portion, as can be seen clearly in the right angular, which has been broken obliquely across the base of the posterior blade. Faint longitudinal striations are present on the lateral surface of the expanded posterior blade of the angular, running parallel to its long axis. The lateral surface of the posterior blade of the angular is flat, although a low longitudinal ridge is present near its ventral border. The sutural surface on the right surangular where the angular has broken away has well-defined borders and striations. This surface scarring on the ventrolateral portion of the surangular is typical for theropods, and suggests that the contact between the surangular and angular was immobile (Currie & Zhao, 1994a: 2054). The posterodorsal-most tip of the posterior process thins to a point and extends toward the mandibular articulation. A very similar condition has been described in the lower jaw of '*Syntarsus*' *kayentakatae* (Tykoski, 1998: 51), and is also present in *Zupaysaurus* (Arcucci & Coria, 2003). The dorsal border of the base of the posterior prong of the angular is distinctly notched at its connection with the more blade-like portion of the surangular. This morphology is also present in '*Syntarsus*' *kayentakatae* (Tykoski, 1998), and probably *Dilophosaurus wetherilli* (UCMP 77270). The posterior tip of the angular clearly extends caudally as far as the surangular foramen, and striations on the ventral side of the posterior surangular and ventrolateral side of the articular suggest that the caudal prong of the angular extended to the end of the jaw articulation, as in '*Syntarsus*' *kayentakatae* (Tykoski, 1998), *Dilophosaurus wetherilli* (UCMP 37302) and *Allosaurus* (Madsen, 1976). Despite the breakage, it is clear

that the caudal splint of the angular completely excluded the surangular from the ventral margin of the lower jaw, as in *Allosaurus* (Madsen, 1976, YPM 14554), 'Syntarsus' kayentakatae (Tykoski, 1998), and *Zupaysaurus* (Arcucci & Coria, 2003).

Both articulars are preserved in contact with the postdentary bones, and can be viewed on the large block from the side containing the posterior skull (Fig. 9). They are massive and form the caudalmost tip of the mandibles. There is no evidence of pneumatism in the articulars. The mandibles have shifted posteriorly relative to the skull, such that the quadrate condyles are not articulated with the mandibular glenoids, and instead are located slightly anterior to them. The articular contacts the surangular laterally and the prearticular anteromedially. The medial mandibular glenoid and the majority of the interglenoid ridge are located on the anterior surface of the articular. The retroarticular process extends posterolaterally from the medial glenoid, as in most theropods (Currie & Zhao, 1994a: 2054). The medial glenoid fossa is cup-shaped and relatively smooth. It is bordered by a low ridge anteriorly, a robust triangular process posteromedially, and rises into a low interglenoid ridge laterally. The large triangular process located posteromedial to the medial glenoid is also present in *Dracovenator*, *Dilophosaurus wetherilli* and *Acrocanthosaurus* (Harris, 1998; Yates, 2005). The foramen chordi tympani (*sensu* Currie & Zhao, 1994a) is typically located anterior to this ridge, but cannot be identified in *Cryolophosaurus*. A smaller, tab-like dorsal process is also present in *Cryolophosaurus* (as well as *Dracovenator*, *Dilophosaurus wetherilli* and *Acrocanthosaurus*), located anterolateral to the retroarticular process (Harris, 1998; Yates, 2005). There is a distinct gap in the posterior wall of the mandibular glenoid, between the triangular posteromedial process and the smaller lateral dorsal process. This gap continues posteriorly onto the dorsal surface of the retroarticular process. A robust, pendant process extends medioventrally from the medial side of the articular. Similar processes are present in many tetanurans, as well as *Dracovenator* and *Dilophosaurus wetherilli* (Yates, 2005).

The retroarticular process is shorter and relatively broader than the condition present in most coelophysoids, such as *Coelophysis bauri*, *Coelophysis rhodesiensis* and 'Syntarsus' kayentakatae (Raath, 1977; Colbert, 1989; Tykoski, 1998). However, the retroarticular process is not as short and broad as in many tetanurans, such as *Allosaurus* (Madsen, 1976), *Giganotosaurus* (MUCPv-CH-1) and *Tyrannosaurus* (Brochu, 2002), where the retroarticular process is broader transversely than the width of the mandible anterior to the glenoid. In these respects the retroarticular process of *Cryolophosaurus* most closely resembles those

of *Dilophosaurus wetherilli* (UCMP 77270) and *Dracovenator* (Yates, 2005). The retroarticular process is transversely broadest at its dorsal surface, and becomes thinner ventrally. The surface of the retroarticular process is relatively flat, and it faces primarily dorsally, but slightly laterally as well, in contrast to the posterodorsally facing retroarticular processes of *Dilophosaurus wetherilli* (UCMP 77270) and *Dracovenator* (Yates, 2005). The edges of the retroarticular process are robust and rounded. They are much more rugose than the weakly concave dorsal surface, possibly reflecting the insertion of the depressor mandibulae muscles (Currie & Zhao, 1994a: 2054).

VERTEBRAL COLUMN

Three articulated posterior cervical vertebrae of *Cryolophosaurus* are preserved on the same block as the skull, and probably represent C6–C8 (Figs 4, 11). Only a small portion of the centrum of the anteriormost of these three vertebrae is preserved (Fig. 4). At least two additional posterior cervicals (probably C9–C10) were recovered during the 2003–04 field season, but have not been completely prepared. They are preserved in articulation with several anterior dorsal vertebrae. The articulated posterior cervicals are associated with several ribs. The left sides of the articulated posterior cervicals are better preserved than the right, and have been prepared more thoroughly. For the following descriptions of vertebral anatomy, the nomenclature for vertebral laminae proposed by Wilson (1999) is adopted.

The last of these three posterior cervical vertebra (~C8) is almost completely preserved. The anterior articular facet is flat, and the posterior facet is concave. The articular facets are both inclined perpendicular to the axis of the centrum, and the the anterior facet is not elevated or canted relative to the posterior facet, suggesting that the neutral posture for the neck was relatively straight at the level of this vertebrae. The rims of the anterior and posterior articular facets are slightly rounded and robust, but not as thick as the articular facet rims of the dorsal vertebrae. The body of the centrum is hourglass-shaped and the articular facets are slightly wider than tall, similar to the condition in *Baryonyx* (BMNH R 9951; Charig & Milner, 1997), *Sinraptor* (Currie & Zhao, 1994a) and carcharodontosaurids (Sereno *et al.*, 1996). A distinct ridge is present on the lateral side of the centrum, running from the middle of the posteromedial part of the left parapophysis to the middle of the posterior articular facet. The dorsoventrally compressed centrum and lateral ridge are very similar to the condition in the posterior cervicals of *Baryonyx* (BMNH R 9951; Charig & Milner, 1997) and *Sinraptor* (Currie & Zhao, 1994a: fig. 14). The left parapophysis is robust and
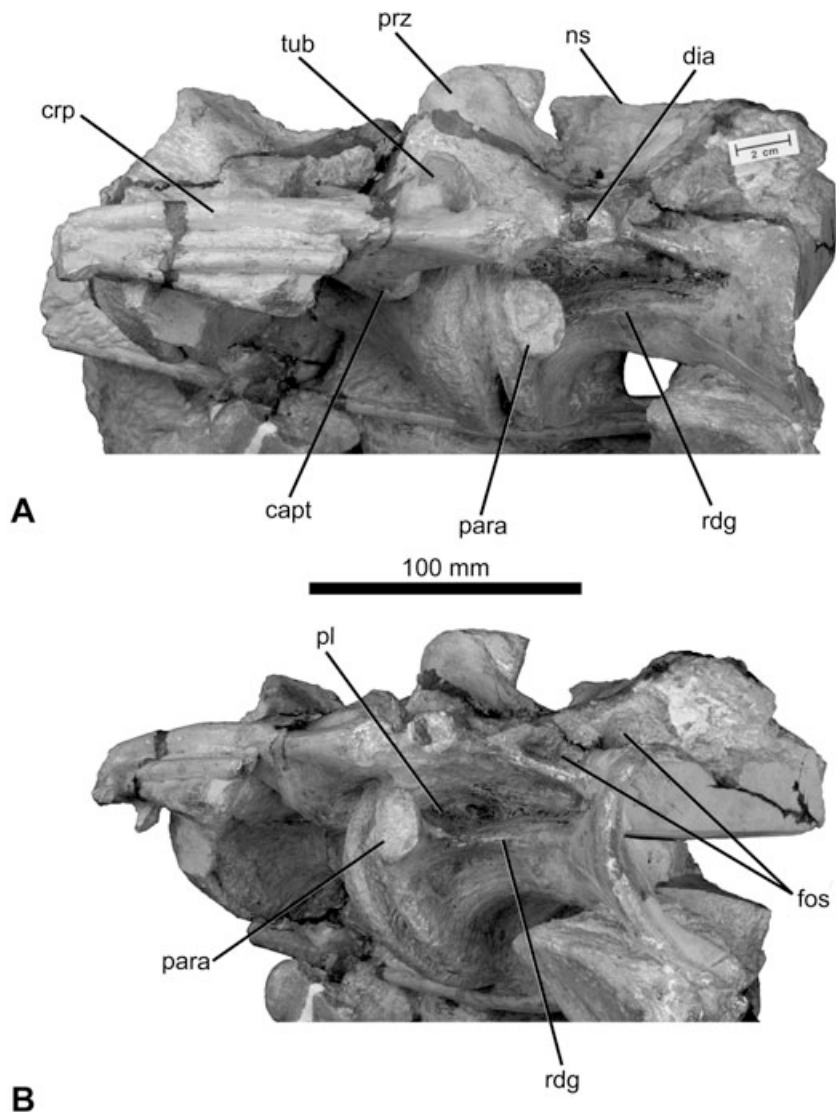
Figure 11. Several articulated posterior cervical vertebrae and ribs of *Cryolophosaurus ellioti* in left lateral (A), and left posterolateral (B), aspects (photo courtesy of J. Weinstein).

slightly oval, and is located anteriorly on the centrum, with its anterior border in contact with the rim of the anterior articular facet of the centrum, as in the posterior cervicals of most theropods. The ventral surface of the centrum is relatively flat and lacks a strong ventral keel.

The dorsal surface of the neural arch is damaged. The anterior and posterior centrodiapophyseal laminae are well developed. The posterior laminae are longer and more inclined than the anterior laminae. A low, broad infradiapophyseal fossa (= 'anterior centrodiapophyseal' and 'posterior centrodiapophyseal' fossae of Wilson, 1999) is present below the transverse process, bounded dorsally by the centrodiapophyseal laminae. The ventral portion of this fossa contains an

anteroposteriorly broad pneumatic fossa extending into the anteromedial portion of the neural arch, excavating a large area dorsomedial to the parapophysis. This pleurocoel is not as sharply rimmed as in most theropods. A low, thin ridge borders the anterior pleurocoel, extending from its dorsal border posteroventrally across the broad infradiapophyseal fossa.

A distinct prezygodiapophyseal lamina (prdl) is present running from the diapophysis to the ventrolateral side of the prezygapophysis. A broad, triangular infrapostzygapophyseal fossa is located posteromedially from the diapophysis. Its anterodorsal border is formed by a robust postzygodiapophyseal lamina, the lateral margin of which has been repaired and touched up with a light brown resin. Its ventral

border is formed by the posterior centrodiapophyseal lamina, and the centropostzygapophyseal lamina makes up its posterior border. The infrapostzygapophyseal fossa opens mainly posterolaterally, and is divided into lateral and medial fossae by a small ridge (Fig. 11). The infrapostzygapophyseal fossa does not appear to possess any distinct foramina, as in abelisauroids and carcharodontosaurids (Carrano *et al.*, 2002; N.D.S. pers. observ.). It is similar in morphology to the infrapostzygapophyseal fossae of the seventh cervical vertebrae of *Dilophosaurus wetherilli* (UCMP 77270) and *Spinostropheus gautieri* (FMNH cast of MNN TIG6; Sereno *et al.*, 2004).

The transverse process is short and extends laterally, and only slightly ventrally, from the base of the neural arch. It is slightly anterior to the middle of the neural arch. It is wider anteroposteriorly at its base than at its tip, due to contributions from the pre-, and postzygodiapophyseal laminae. The costal facet is oval-shaped with an anteroposterior long axis.

The prezygapophysis extends anterodorsally from the lateral side of the neural arch. The lateral side of its stalk grades smoothly into the anteromedial base of the transverse process, along the prezygodiapophyseal laminae. The prezygapophysis is inclined medially for its articulation with the postzygapophysis from the preceding vertebrae. A robust spinoprezygapophyseal lamina extends from the posteromedial portion of the prezygapophyseal articular facet to the anterolateral base of the neural spine. The postzygapophysis extends posterodorsally from the lateral side of the neural arch, just medial to the posterior base of the transverse process. Its pedicel is relatively longer than that of the prezygapophysis, and the postzygodiapophyseal lamina extends from the diapophysis to the lateral side of the middle of the pedicel. The distal end of the pedicel angles posteriorly and widens into the articular facet of the postzygapophysis. The articular facet is robust and inclined laterally.

An epipophysis is located on the dorsal surface of the postzygapophysis. Despite incomplete preservation, the epipophysis does not appear to be as robust dorsoventrally as in many tetanuran theropods such as *Allosaurus* (Madsen, 1976) and *Sinrapor* (Currie & Zhao, 1994a: figs 13, 14), although this may be indicative of the posterior position of the vertebrae in the cervical series (see difference in robustness of epipophyses in mid-posterior cervicals of *Sinraptor*; Currie & Zhao, 1994a: figs 13, 14). In general, the epipophyses of theropods are more strongly developed in the anterior cervicals where they serve as robust attachment points for intersegmental muscles that hold up the skull (Currie & Zhao, 1994a: 2057).

The neural spine extends dorsally from the middle of the neural arch. Only the base of the neural spine is preserved, but it appears to be short anteroposteriorly,

which is consistent with the morphology of the posterior cervical neural spines of theropods.

Most of the mid-posterior part of the dorsal vertebral column of *Cryolophosaurus* has been recovered, and several articulated anterior dorsal vertebrae were recovered in 2003–04, but have yet to be prepared from a large block. Most of the preserved dorsal vertebrae are characterized by hourglass-shaped centra with amphiplatyan articular facets (Fig. 12). The rims of the articular facets are robust and bear striations, as are present in the cervicodorsals of most theropods. The facets are generally oval in anterior or posterior view, and tend to be slightly higher than wide. No pleurocoels are present on any of the middle or posterior dorsals. A slight ventral keel is only present in what may be the posteriormost dorsal. It is not similar to the extremely robust ventral keels present in the anterior dorsals of many tetanurans (Rauhut, 2003). The remaining vertebrae described have centra with rounded ventral surfaces.

The neural arches are completely fused to the centra in all the dorsals. The transverse processes extend dorsally from their neural arches at an angle of approximately 45 . They are roughly triangular in dorsal view and swept slightly posteriorly. The posterior centrodiapophyseal laminae are robust and preserved in most of the dorsals. The neural spines, where preserved, are thin mediolaterally and long anteriorposteriorly. They extend dorsally, either straight, or with a slight posterior inclination, from the mid-posterior half of the neural arch. The prezygapophyses are situated close to the midline and their articular facets are orientated dorsally and slightly medially. The parapophyses migrate dorsally on the neural arch as one moves posteriorly through the dorsal vertebral column, as in most archosaurs (Rauhut, 2003). The infraprezygapophyseal, infradiapophyseal and infrapostzygapophyseal fossae are distinct and relatively deep, with the latter two fossae relatively larger. The infraprezygapophyseal fossae decrease in area posteriorly in the dorsal vertebral column, as a consequence of the dorsal migration of the parapophyses. Paradiapophyseal laminae are well developed (Fig. 12E, F). In several of the mid-posterior dorsals, the parapophyses extend laterally on a stalk (Fig. 12A–F), similar to the condition in *Dilophosaurus wetherilli* (Welles, 1984), *Piatnitzkysaurus* (MACN CH 895) and several neoceratosaurs (Carrano *et al.*, 2002). The postzygapophyses are situated close to the midline, with their articular facets orientated ventrally and slightly laterally. Their medial borders abut each other and curve ventrally into a hyposphene, which is situated directly above the posterior opening of the neural canal. A hyposphene–hypantrum articulation is present in all dorsal vertebrae, and the hyposphenes tend to be more robustly developed in the posterior elements.
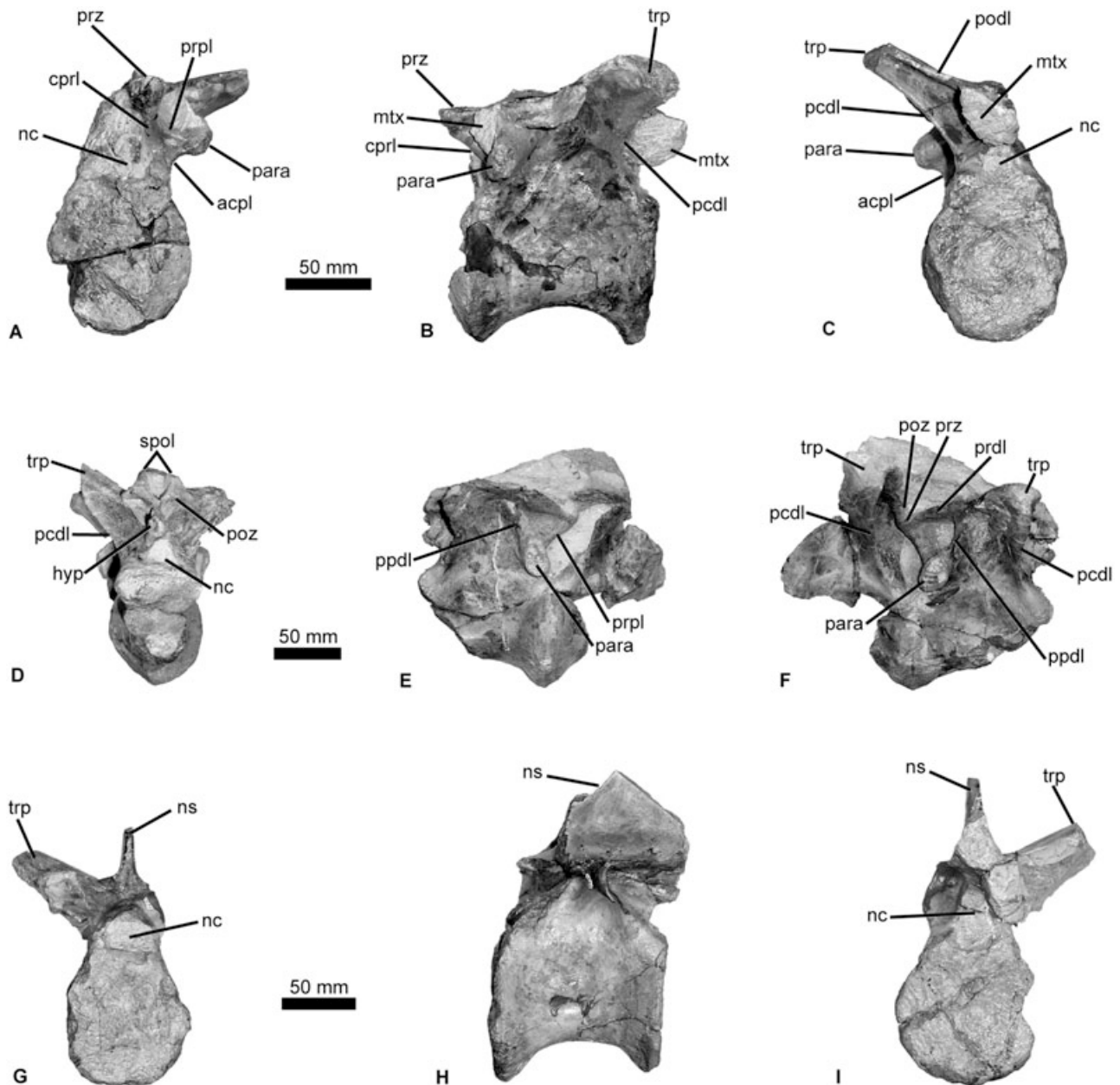
Figure 12. Mid-posterior dorsal vertebra (~D7–13) of *Cryolophosaurus ellioti* in anterior (A), left lateral (B) and posterior (C) aspects. Two articulated posterior dorsal vertebrae (> D9) of *Cryolophosaurus ellioti* in posterior (D), right lateral (E) and left lateral (F) aspects. Posterior dorsal vertebra (~D14) of *Cryolophosaurus ellioti* in anterior (G), left lateral (H) and posterior (I) aspects.

An extremely well-preserved vertebra probably represents the fifth sacral vertebrae (= 'caudosacral 1' of Welles, 1984). Both sacral ribs are completely preserved, as well as most of the base of the neural spine (Fig. 13A–D). The sacral ribs are fused to the dorsal half of the centrum and the bases of the transverse processes with no clear traces of sutures. The large, robust neural arch is completely fused with the centrum. Overall the element bears much similarity to

the fifth sacral vertebrae of *Dilophosaurus wetherilli* (UCMP 37302; TMM 43646-60, see Tykoski, 2005: fig. 52), *Piatnitzkysaurus* (MACN CH 895) and *Allosaurus* (Gilmore, 1920: pl. 8; Madsen, 1976: pl. 27).

The centrum is waisted, but not as hourglass-shaped as in the dorsal vertebrae. A weak keel is present on the ventral surface. No pleurocoels are present on the centrum. The anterior articular facet of the centrum is vertically oval, while the posterior
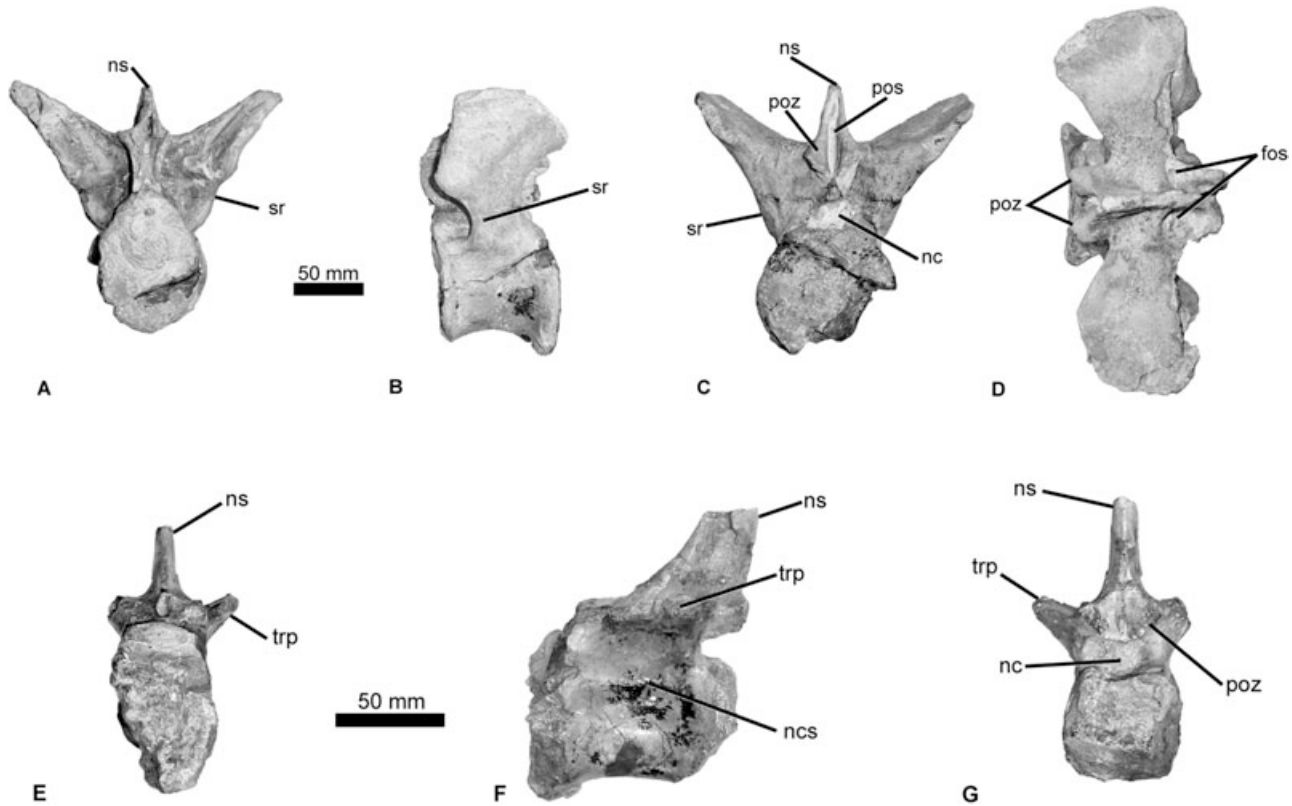
Figure 13. Fifth sacral vertebra (= 'caudosacral 1') and fused sacral ribs of *Cryolophosaurus ellioti* in anterior (A), left lateral (B), posterior (C) and dorsal (D) aspects. Anterior–middle caudal vertebra of *Cryolophosaurus ellioti* in anterior (E), left lateral (F) and posterior (G) aspects.

articular facet is more circular. No evidence of fusion to the preceding vertebra is evident on its anterior surface, which may suggest that the individual represents a subadult. The posterior articular facet is also set slightly more ventrally than the anterior articular facet. The rims of the articular facets of the centrum are very robust, and the posterior rim of the articular facet is significantly more robust and well developed than the rim of the anterior articular facet, as in *Piatnitzkysaurus* (PVL 4703), and *Allosaurus* (Gilmore, 1920: pl. 8; Madsen, 1976: pl. 27).

Although the anteriormost portion of the neural arch is not completely preserved, a distinct prespinal fossa is present. This fossa is bound by spinoprezygapophyseal laminae, which are widely separated at their base. Both laminae curve posterodorsally into the neural spine above the prespinal fossa. Dorsoventrally tall centroprezygapophyseal laminae are also present on the anterior neural arch. They curve ventromedially from the base of the obliterated prezygapophyses into the top of the anterior articular facet of the centrum, turning slightly laterally just before reaching the top of the centrum. The centroprezyapophyseal laminae are thus slightly concave laterally. There are two, roughly circular and shallow fossae

present on the anterior part of the neural arch, lateral to the anterior base of the neural spine (Fig. 13D). Similar fossae are present on the anterodorsal portion of the fifth sacral neural arch of *Piatnitzkysaurus* (PVL 4703), and probably represent vestigial infraprezygapophyseal fossae.

The sacral rib and lateral portion of the neural arch are fused into an extremely robust element. They are relatively thinner anteroposteriorly (roughly have the length of the centrum), at their ventral base, and have a short 'neck' before expanding anteroposteriorly and becoming fan-shaped (Fig. 13B). This is similar to the morphology of the fifth sacral of *Allosaurus* (Gilmore, 1920: pl. 8; Madsen, 1976: pl. 27), *Dilophosaurus wetherilli* (UCMP 37302) and *Piatnitzkysaurus* (PVL 4703). The fused sacral rib is angled dorsally at approximately 45 . The base and 'neck' of the process extends laterally from the neural arch, but the expanded, fan-shaped distal end is swept slightly posteriorly. The blade-shaped distal end of the transverse process is most similar in morphology to that of *Piatnitzkysaurus* (PVL 4703), and its posterodorsal tip is not expanded posteriorly as in *Dilophosaurus wetherilli* (UCMP 37302). The degree of posterior inclination of the transverse process, and its corresponding artic-

ulation with the medial iliac blade, could reflect the degree of incorporation of the fifth sacral into the sacral series in these taxa. As in *Dilophosaurus wetherilli* (UCMP 37302), and *Piatnitzkysaurus* (PVL 4703), the anterior corner of the expanded, fused transverse process and sacral rib lacks the distinct, hook-like process present in the fifth sacral of *Allosaurus* (Gilmore, 1920: pl. 8; Madsen, 1976: pl. 27).

The postzygapophyses are situated very close to the midline, such that their ventral edges slightly abut each other. The articular facets of the postzygapophyses face ventrolaterally. Spinopostzygapophyseal laminae extend from the posterodorsal portion of the postzygapophyses posterodorsally to border a deep, vertically elongate postspinal fossa. The area immediately ventral to the postzygapophyses is not well preserved, but a weak hyposphene may have been present.

Many complete and partial caudal vertebrae from *Cryolophosaurus* have been recovered. Most represent elements from the anterior mid-caudal region, though a partial centrum of what may represent the first caudal has also been recovered. Five anterior mid-caudals are preserved in a block in articulation with each other, as well as their three posteriormost chevrons. Only the first two of these caudals are near complete; the neural arches of the remaining caudals have been broken off. The best-preserved element of the caudal series probably represents an anterior mid-caudal (Fig. 13E–G). The centrum is slightly waisted, but is not as hourglass-shaped as the dorsal vertebrae. The ventral surface is rounded and does not bear a distinct keel or furrow. The surfaces of the rims of the articular facets of the centrum are not well preserved, but they appear to be fairly robust. The centrum is longer than high, and its articular surfaces are amphiplatyan. The neurocentral suture is closed, but not completely fused, and the suture can still be traced on the lateral surface of the centrum (Fig. 13F).

The neural spine is anteroposteriorly and mediolaterally thin, and swept back posterodorsally. The posterior border of the neural spine extends straight dorsally with a slight posterior inclination from above the posterior articular facet of the centrum. The anterior border starts at the middle of the anterior half of the centrum, and extends posteriorly at its base, staying fairly low dorsally. As it extends posteriorly it slowly arcs more dorsally until its border is parallel to the posterior border of the neural spine (Fig. 13F). The inclination of the neural spine is similar to that present in *Poekilopleuron bucklandii* (Allain & Chure, 2002), and appears to be intermediate to that seen in the mid-caudals of *Allosaurus* (Madsen, 1976), where the neural spines are swept back strongly posteriorly, and that of *Ceratosaurus* (Madsen & Welles, 2000), where the neural spines of the mid-caudals rise

directly dorsally from the neural arch. No anterior spike-like process appears to have been present.

Only the bases of the transverse processes are preserved. They extend laterally from the neural arch and are angled dorsally at least 35 , but less than 45 , making their dorsal inclination not as extreme as in more anterior vertebrae. The transverse processes are thin dorsoventrally, and at their base are about as long anteroposteriorly as the main body of the centrum (minus the robust articular facets). The articular facets of the postzygapophyses face ventrolaterally. A small, dorsoventrally elongate elliptical fossa appears to be present medially between the postzygapophyses.

Several posterior cervical ribs are preserved in association with two articulated posterior cervical vertebrae. These elements are preserved on the same block as the skull. The body and shafts of the ribs are convex laterally. The capitula are directed ventromedially from the body of the ribs, and are located slightly anterior to the dorsomedially directed tubercula. Shallow medial excavations are present anterior and posterior to the capitula and tubercula. These bear some resemblance to the degree of cervical rib excavation present in *Dubreuillosaurus* (Allain, 2005). The ribs have extremely elongate cranial processes, as in *Coelophysis bauri* (Colbert, 1989), *Coelophysis rhodesiensis* (Raath, 1977; Colbert, 1989), '*Syntarsus*' *kayentakatae* (Tykoski, 1998) and *Spinostropheus gautieri* (FMNH cast of MNN TIG6; Sereno *et al.*, 2004). These cranial processes extend as thin spines forward under those of the preceding vertebrae, forming bundles that are superficially similar to the bundles formed by the posterior rib spines in taxa such as *Coelophysis bauri* (Colbert, 1989), *Coelophysis rhodesiensis* (Raath, 1977; Colbert, 1989), '*Syntarsus*' *kayentakatae* (Tykoski, 1998) and *Spinostropheus gautieri* (FMNH cast of MNN TIG6; Sereno *et al.*, 2004) (Fig. 11).

Several isolated dorsal ribs have been recovered that are probably attributable to *Cryolophosaurus*. None of these elements is complete, however, and little can be said concerning their morphology. The ribs are more two-dimensional, and the capitula and tubercula are more widely spaced, as is typical for theropod dorsal ribs. The ribs appear to be simple and apneumatic, exhibiting no morphological features that are diagnostic of more inclusive groups within Theropoda.

Chevrons are preserved in articulation with several mid-caudals. Overall, the mid-caudal chevrons closely resemble those of basal theropods, such as *Dilophosaurus wetherilli* (UCMP 37302) or *Ceratosaurus* (Madsen & Welles, 2000). The chevrons extend ventrally from their articulations with the ventral surfaces of the mid-caudal centra, and curve slightly posteriorly, with the angle of the posterior curve increasing distally along the chevron. The chevrons are very thin and rod-like, though they are slightly

thicker anteroposteriorly than mediolaterally. The proximal ends of the chevrons expand slightly mediolaterally at their articular surfaces. The short anterior processes typical of tetanurans and neoceratosaurs are not present on any of the recovered chevrons. The distal ends are only slightly expanded anteroposteriorly and do not resemble the L-shaped morphology seen in many tetanurans.

APPENDICULAR SKELETON

Elements of the forelimb recovered include the proximal and distal ends of the left humerus, and the proximal ends of both the right ulna and right radius. The humeral head is rugose and transversely elongate, as in most theropods with the exception of *Elaphrosaurus* and abelisauroids (Rauhut, 2003). The internal tuberosity extends posteromedially from the medial surface of the humerus as a robust flange, with an oval-shaped rugosity at its tip facing posteromedially and slightly dorsally (Fig. 14A, B). If the internal tuberosity is homologous with the bicipital crest of birds, then this rugosity may have served as the attachment point for the aponeurosis of the humeral head of M. biceps brachii (Baumel & Witmer, 1993; Makovicky & Sues, 1998). The internal tuberosity is set slightly below the level of the humeral head, and there is a shallow notch separating their articular surfaces. The distal portion of the left humerus preserves both distal condyles, which are rounded and face slightly anterior relative to the humeral shaft as in most theropods (Fig. 14C, D). The ulnar condyle is slightly broader mediolaterally and anteroposteriorly than the radial condyle. A small anterior groove separates the two condyles and expands proximally into a shallow fossa on the anterior face of the distal humerus.

The proximal end of the right ulna is expanded anteroposteriorly and transversely flattened relative to the condition in most theropods (Fig. 14E, F). The olecranon process is large and mound-shaped, similar to the ball-shaped olecranon processes of *Piatnitzkysaurus* (PVL 4073), and *Dilophosaurus wetherilli* (UCMP 37302), though the process is higher in the former taxon. The triangular anterior process is similar to those of '*Szechuanosaurus*' *zigongensis* (Gao, 1998) and *Dilophosaurus wetherilli* (UCMP 37302).
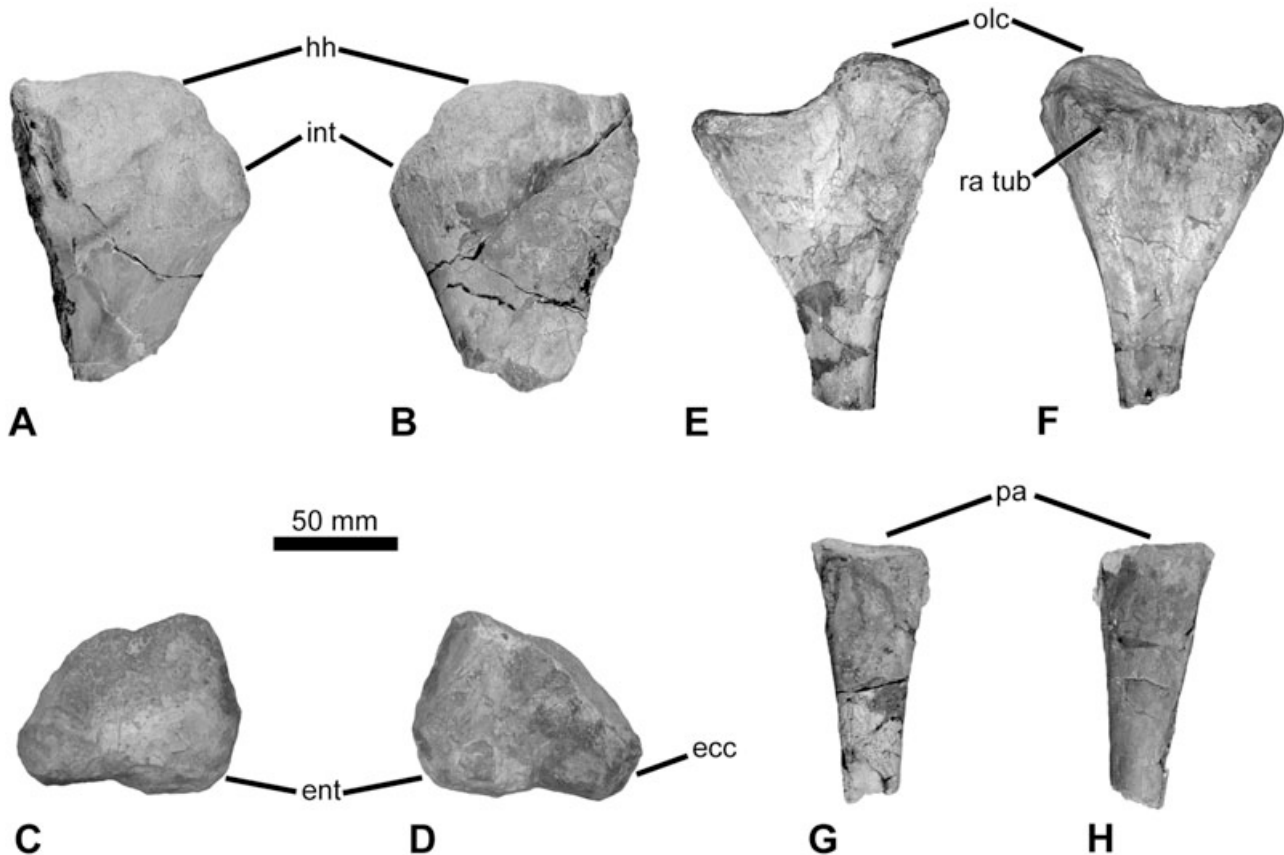
Figure 14. Proximal and distal left humerus of *Cryolophosaurus ellioti* in posterior (A, C) and anterior (B, D) aspects. Proximal right ulna of *Cryolophosaurus ellioti* in medial (E) and lateral (F) aspects. Proximal right radius of *Cryolophosaurus ellioti* in medial (G) and lateral (H) aspects.

The proximal articular surface of the ulna is roughened and rugose. This rugosity is developed as distinct proximal rims that can be seen in lateral and medial aspect. A radial tuberosity is developed on the lateral side of the proximal ulna, distal to the olecranon process. Faint longitudinal striations are present on the lateral and medial fossae formed by the triangular anterior process of the ulna below these rims. These striations run parallel to the long axis of the triangular anterior process. The shaft of the ulna is relatively not as thick as it is in *Allosaurus* (Madsen, 1976), *Piatnitzkysaurus* (PVL 4073) or '*Szechuanosaurus*' *zigongensis* (Gao, 1998), and resembles that of *Dilophosaurus wetherilli* (UCMP 37302). The shaft is hollow and roughly triangular with rounded edges in cross-section.

The broken end of the right radius also reveals a hollow shaft. The proximal end is slightly expanded anteroposteriorly and bears a small raised tip at its anterior edge. The proximal articular surface is distinctly cup-shaped for articulation with the radial condyle of the humerus (Fig. 14G, H). The shaft of the radius is weakly elliptical in cross-section, with a slightly longer anteroposterior axis. The lateral surface is convex, while the medial surface is relatively flat.

The majority of the left ilium is preserved, though many areas are damaged and have been glued or repaired (Fig. 15). The ilium anterior to the supraac-etabular crest is missing, including the pubic peduncle. The anteroventralmost portion of the acetabulum is also missing, as is the posterodorsalmost end of the ilium, though in general the brevis shelf is well preserved. The long postacetabular blade of the ilium is almost completely intact. Interpretation is difficult due to the missing anterior portion of the ilium and a large piece dorsal to the supraacetabular crest that has been glued out of position, but it appears that the dorsal border of the ilium was fairly straight, or only slightly convex in lateral view.

The supraacetabular crest takes the form of a thick, laterally extensive and ventrally concave hood. Although the supraacetabular shelf is large, it does not appear to extend as far posteriorly as it does in *Dilophosaurus wetherilli* (UCMP 37302), where it extends slightly further than the posterior border of the ischial peduncle in ventral aspect (though in TMM 43646-60 the acetabular shelf does not appear to extend quite this far posteriorly). The supraacetabular crest is not confluent with the lateral brevis shelf, as in the basal theropods *Coelophysis bauri* (UCMP 129618) and *Coelophysis rhodesiensis* (QG 1, QG 691; see Raath, 1990: fig. 7.5).

The ischial peduncle projects posteroventrally at an angle of less than 45 from the ventral ilium. In distal view, the articular facet of the ischial peduncle takes the form of a weakly equilateral triangle, with its base at the posterior end of the peduncle and its apex ante-
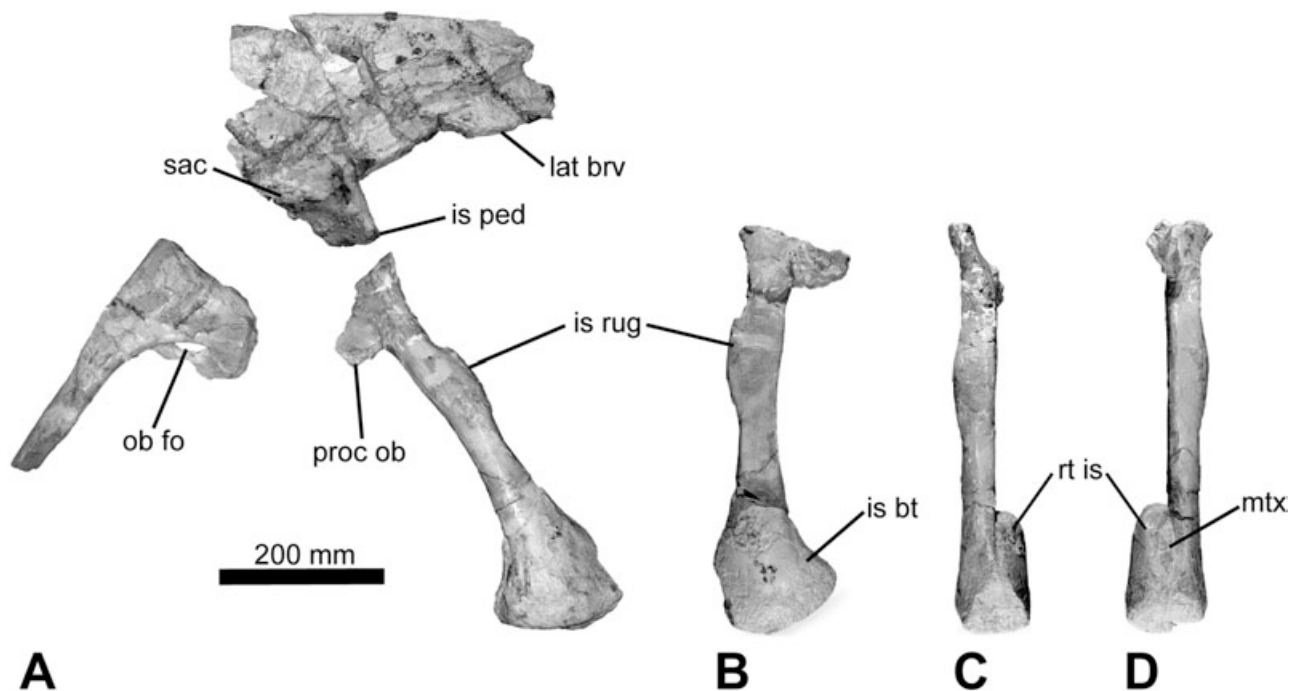
Figure 15. Left ilium, pubis and ischium of *Cryolophosaurus ellioti* in lateral (A) aspect, and left and right ischia of *Cryolophosaurus ellioti* in medial (B), posterior (C) and anterior (D) aspects.

riorly. Both the anteromedial and the anterolateral borders of the ischial peduncle are slightly concave in distal aspect, such that the anterior apex of the ischial peduncle is pointed, while the posterolateral and posterodorsal corners are more robust and rounded. The concavity of the anterolateral border of the ischial peduncle flows smoothly proximally into the acetabulum. The ischial peduncle is similar to that of *Dilophosaurus wetherilli* (UCMP 37302), although in this taxon the anteromedial and anterolateral borders are not concave, and the posterior border is strongly convex, in distal view. The basal tetanurans *Piatnitzkysaurus* (PVL 4073) and '*Szechuanosaurus*' *zigongensis* (Gao, 1998) also retain a similar morphology. The ischial peduncle is fairly large relative to the acetabulum, which is unlike the condition in tetanurans such as *Allosaurus* (YPM 4944), where the ischial peduncle of the ilium is reduced anteroposteriorly, and more D-shaped than triangular.

Most of the lateral and medial shelves of the brevis fossa are preserved on the ventral portion of the postacetabular blade. The posteriormost portion of the ilium is broken and missing such that the posterior end of the ilium can be viewed in cross-section. The brevis fossa is fairly narrow in ventral view, as in most theropods with the exception of coelophysoids, neoceratosaurs and several ornithomimids, which possess brevis fossae that are expanded substantially posteriorly. The lateral shelf of the brevis fossa is deeper ventrally than the medial shelf, similar to the condition present in most theropods, with the exception of *Eustreptospondylus*, *Afrovenator* and *Torvosaurus*, in which the opposite is true. The lateral brevis shelf extends lateroventrally from the posterior dorsal blade of the ilium. The medial brevis shelf extends medioventrally from the posterior blade at approximately the same angle as the lateral shelf.

The proximal half of the left pubis is preserved, and it is similar in appearance to that of *Dilophosaurus wetherilli* (TMM 43646-60; Tykoski, 2005), *Piatnitzkysaurus* (MACN CH 895) and *Condorraptor* (MPEF-PV 1696). The proximal end of the pubis is not 'kinked' for its articulation with the pubic peduncle of the ilium, as in many coelophysoids (Rauhut, 2003). A completely enclosed obturator foramen is present slightly anterior to the ischiadic peduncle (Fig. 15). Parts of the proximal pubis around the obturator foramen have been plastered and glued, but smooth, rounded bone is still intact surrounding the opening on its lateral side. The foramen opens anteroventrolaterally and is oval-shaped with its long axis running anteroposteriorly.

Ventral to the obturator foramen the bone is damaged and broken. An additional pubic fenestra below the obturator foramen has traditionally been considered characteristic of ceratosaurs (*sensu* Gauthier,

1986), though the exact distribution of this character is difficult to determine due to the delicate nature of this area of the pubis and damage to this area in various specimens (i.e. *Cryolophosaurus*, *Piatnitzkysaurus* and *Condorraptor*). However, Rauhut (2005a: 101) notes that although the subacetabular plate of the pubis is not completely preserved in *Condorraptor*, there is not enough space for the ventral expansion of the plate that would be required to accommodate a pubic fenestra. This appears to be the case for *Cryolophosaurus* as well.

Anterior to the ventral border of the subacetabular plate and on the anterolateral border of the pubic shaft is a distinct pubic tubercle, which probably served as the origin of M. ambiens (Hutchinson, 2001a). The tubercle is similar in position to that of other basal tetanurans such as *Piatnitzkysaurus* (MACN CH 895; PVL 4073), *Condorraptor* (MPEF-PV 1696) and *Allosaurus* (YPM 4944). However, the pubis of *Cryolophosaurus* does not exhibit a marked medial kink at the level of the pubic tubercle in anterior aspect, as it does in these taxa, and also *Ceratosaurus* (Gilmore, 1920). Beginning at the distal end of the pubic tubercle, the shaft of the pubis expands mediolaterally to form a pubic apron. As is noted for other theropods (Rauhut, 2005a: 101), the pubic apron is confluent with the anterior surface of the pubic shaft, such that the pubic shaft extends out beyond the pubic apron posteriorly.

The entire left ischium is preserved except for the proximalmost portion (Fig. 15). Only the ischial 'boot' of the right ischium is preserved, contacting its counterpart. Although the proximal end of the ischium is damaged and not completely preserved, an extensive puboischiadic plate (as in coelophysoids and *Ceratosaurus*) does not appear to have been present. The ischial shaft thickens posterolaterally into a short, elongate and extremely robust crest, starting about one-quarter of the ischial length from the proximal end and thinning again slightly past one-half the ischial length from the proximal end of the bone (Fig. 15). Although the left ischial shaft would have been closely conjoined with its right counterpart at the level of this crest, as indicated by its flat, medial articular surface (Fig. 15B), it is unclear if the ischial crests would have functioned as a joint median tuberosity. A similar well-developed posterior ischial crest is present in *Sinraptor* (Currie & Zhao, 1994a: fig. 21). Currie & Zhao (1994a: 2069) note that similarly well-developed crests are present in *Acrocanthosaurus*, *Allosaurus*, *Yangchuanosaurus* and *Megalosaurus*, though the crests in *Acrocanthosaurus* and *Allosaurus* may be more weakly developed (Stovall & Langston, 1950: 717–718). A slightly less well-developed posterior ischial crest is also present in *Dilophosaurus wetherilli* (TMM 63646-60; Tykoski, 2005). Currie &

Zhao (1994a: 2069) suggested that this crest may have served as the origin for powerful adductor musculature in *Sinraptor*. However, Hutchinson (2001a) tentatively suggested that this structure might be associated with the M. flexor tibialis group.

A well-defined ischial 'boot' is present, which is approximately three times as wide as the anteroposterior width of the ischial shaft. The posterodorsal portion of the boot is only expanded slightly, with most of the expansion from the ischial shafts being anteroventral. This anterior expansion is not as extensive as in the basal theropods *Ceratosaurus* (Gilmore, 1920) and '*Szechuanosaurus*' *zigongensis* (Gao, 1998), and most closely resembles the condition in *Dilophosaurus wetherilli* (TMM 43646-60; Tykoski, 2005). The ischia contact distally at the 'boot', and the posterodorsalmost portion of the 'boot' is incompletely preserved. The distal conjoined ischia are only slightly thicker mediolaterally than the ischial shafts. Anteriorly, both portions of the ischial boots end in slightly rounded knobs, which contact medially. A similar morphology is present in *Piatnitzkysaurus* (MACN CH 895). A shallow, elongate, elliptical fossa is present proximal to the fused knobs, partially filled in by matrix (Fig. 15D).

The right femur is partially preserved in two pieces, the proximal of which is less damaged (Fig. 16A, B). The left femur is relatively complete, but has been extensively repaired (Figs 16, 17). A large crack separates the caput of the femur from the shaft, and has been plastered. The left femur is strongly sigmoidal in anterior aspect, as in *Dilophosaurus wetherilli* (UCMP 37302). The femoral shaft is bowed anteriorly as in other basal theropods, such as '*Syntarsus*' *kayantakatae* (Tykoski, 1998) and *Ceratosaurus* (Madsen & Welles, 2000). The femoral head is directed 40–45° anteromedially. In proximal view, the greater tro-

chanter narrows from medial to lateral. A shallow, proximal articular groove (*sensu* Carrano *et al.*, 2002) runs mediolaterally across the proximal femur. The femoral head has a very distinct medial, posteriorly curving lip, which bounds the oblique ligament groove medially.

The lesser trochanter is weakly developed compared with tetanuran theropods, and is partially damaged in both femora. The lesser trochanter is placed relatively low on the lateral side of the proximal femur, below the level of the greater trochanter and the femoral head (Fig. 16A). This is similar to the 'intermediate' position of the lesser trochanter relative to the femoral head described by Carrano (2000). The proximalmost preserved portion of the lesser trochanter is approximately 95 mm below the proximal end of the femur. The lesser trochanter is a rounded, 'finger-like' projection, similar in morphology to *Dilophosaurus wetherilli* (UCMP 37302). A damaged trochanteric shelf is present distal and posterolateral to the lesser trochanter.

The fourth trochanter is well developed as an oblong crest on the posteromedial side of the proximal femoral shaft (Fig. 17B, C). It is more prominent than the fourth trochanter of *Allosaurus* (YPM 4944; Madsen, 1976). The fourth trochanter is slightly concave medially, allowing for the insertion of M. caudofemoralis longus (Currie & Zhao, 1994a: 2069).

The distal femur has a prominent crista tibiofibularis and medial epicondyle. The anterior face of the distal femur is flat and relatively unmarked. It does not bear a distinct extensor groove (Fig. 16D), as is present in many tetanurans, with the exception of *Dubreuillosaurus* (Allain, 2005). The distalmost portion of the femur is poorly preserved, and it is difficult to ascertain if the distal condyles are flat, as in basal theropods, or
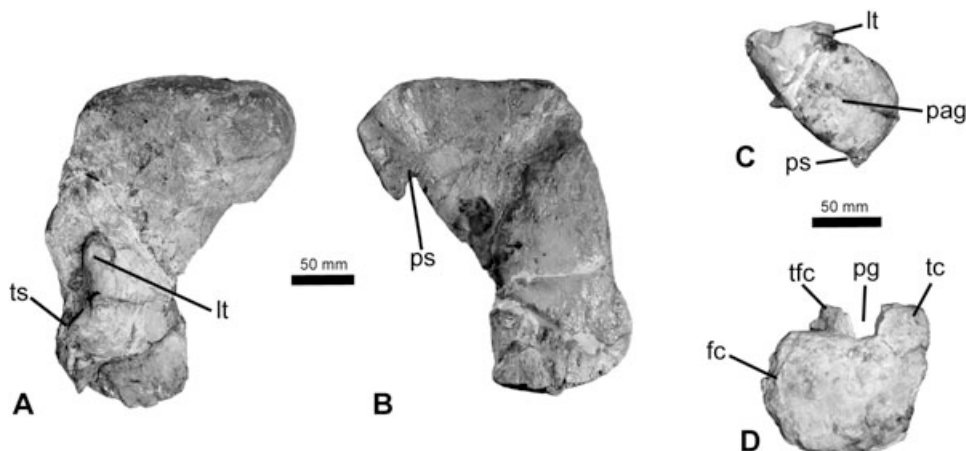

Figure 16. Proximal right femur of *Cryolophosaurus ellioti* in anterior (A) and posterior (B) aspects. Left femur of *Cryolophosaurus ellioti* in proximal (C) and distal (D) aspects. Anterior is to the right in Figure 15C, and toward the bottom in Figure 15D.
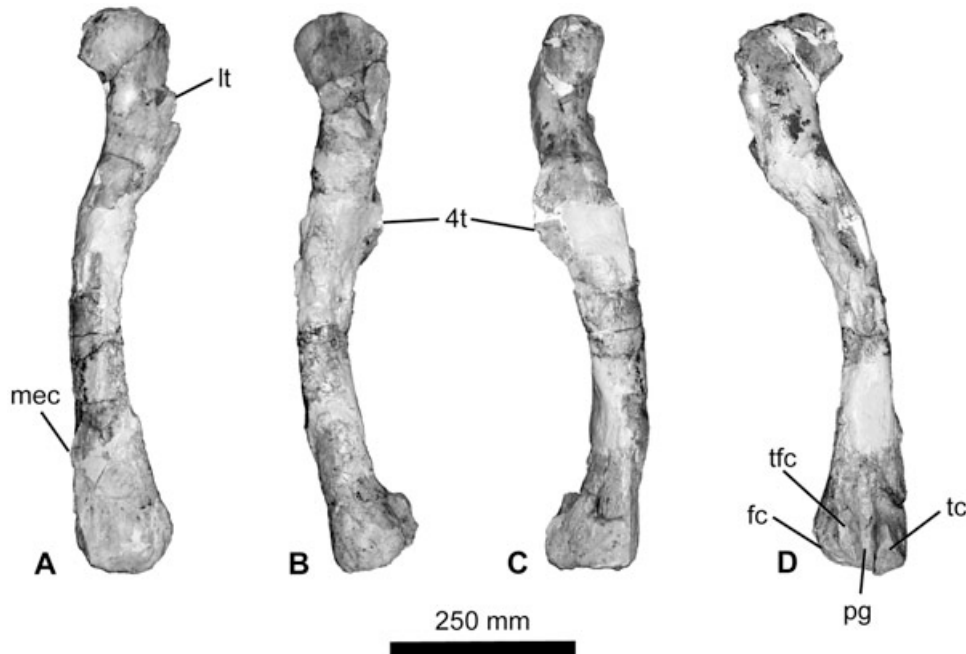
Figure 17. Left femur of *Cryolophosaurus ellioti* in anterior (A), lateral (B), medial (C) and posterior (D) aspects.

more rounded as is present in neoceratosaurs and tetanurans (Rauhut, 2003). The medial epicondyle of the distal femur is roughly triangular in posterior view, and is deep anteroposteriorly. Small portions of the posterior, medial and distal part of the medial epicondyle are missing. A conspicuous ridge extends proximally from the proximal end of the condyle. This low, thin ridge extends up the middle of the posterior femoral shaft. This ridge is similar to those present in *Condorraptor* (MPEF-PV 1691) and *Sinraptor* (Currie & Zhao, 1994a: fig. 22), and is probably the 'adductor ridge' of Hutchinson (2001b). A medial epicondylar ridge is present on the medial side of the anterior distal femur (Fig. 17A). It is most similar to that of basal tetanurans, and does not exhibit the hypertrophied morphology present in abelisauroids such as *Masiakasaurus* (FMNH PR 2123; Carrano *et al.*, 2002). Only the proximalmost portion of the medial epicondylar ridge is preserved, but it is very distinct. The ridge extends at a low angle mediodistally from the anterior surface of the distal femur. The distal two-thirds of the flange has been broken and is missing. The crista tibiofibularis is also distinct, despite being incompletely preserved. The crest lies lateral to the medial epicondyle on the posteromedial face of the lateral condyle of the femur, and is slightly inset proximally from the distal end of the femur. Its long axis runs from dorsolateral to ventromedial. As in most theropods the lateral condyle of the distal femur is well developed and bulbous in distal aspect, giving the distal femur a lateral convexity. The medial side of the distal femur is
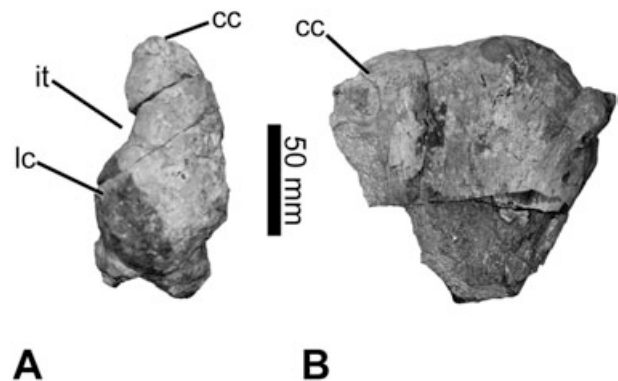
Figure 18. Proximal left tibia of *Cryolophosaurus ellioti* in proximal (A) and lateral (B) aspects.

relatively flat, and is continuous with the medial surface of the tibial condyle. A distinct posterior intercondylar groove is also present on the posterior side of the distal femur. This groove does not appear to extend onto the distal surface of the femur, and there is no infrapopliteal crest traversing it, as in several coelophysoids and neoceratosaurs (Tykoski, 2005).

Only the distal portion of the left tibia is preserved, along with a fragmentary element that may represent the proximal end (Figs 18, 19). This proximal fragment of the tibia is badly damaged, and does not preserve fine detail of the tibial morphology. The distal portion of the left tibia is preserved in contact with the distal left fibula and left astragalus and calcaneum.
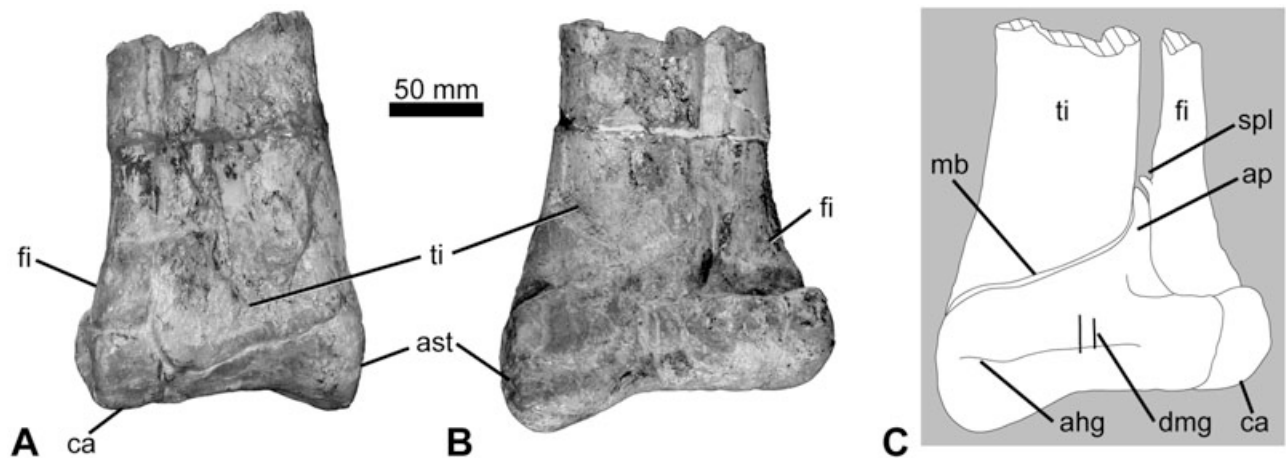
Figure 19. Left tibia, fibula, astragalus and calcaneum of *Cryolophosaurus ellioti* preserved in articulation in posterior (A) and anterior (B) aspects, and interpretive line drawing of anterior aspect (C) (photos courtesy of ReBecca Hunt).

Though damaged, in proximal aspect the tibia resembles that of most basal theropods. The fibular condyle tapers medially into the cnemial crest, which is offset from the fibular condyle laterally by a shallow incisure (Fig. 18A, B). This indention is not as well developed as in most tetanurans, which have a well-developed incisura tibialis that is roughly rectangular in proximal aspect (Rauhut, 2003, 2005a). No fibular crest is present on the lateral side of the proximal tibia, which may suggest that this crest was located more distally, as in many tetanurans (Rauhut, 2003, 2005a: fig. 24B). The cnemial crest does not extend as far anteriorly as in the neoceratosaurs *Ceratosaurus* (YPM 4681), *Genusaurus* (Accarie *et al*., 1995) and *Masiakasaurus* (Carrano *et al*., 2002). The cnemial crest is slightly rounded in lateral view, as opposed to the more rectangular appearance in most theropods. This is similar to the condition in the basal tetanuran *Condorraptor* (MPEF-PV 1690). The posterior portion of the tibia is damaged and it is difficult to ascertain whether a distinct cleft (= 'posterior intercondylar groove' of Carrano *et al*., 2002) between the medial portion of the proximal tibia and the fibular condyle exists, as is present in most other theropods, with the exception of the basal tetanuran *Condorraptor* (MPEF-PV 1690). The rounded edge of the posterior portion of the fibular condyle suggests that such a cleft was present, however.

The distal end of the tibia is mediolaterally expanded as is typical in most theropods, but it is difficult to determine the exact proportion of this expansion (i.e. anteroposterior width vs. mediolateral width of distal tibia). The lateral side of the distal tibia extends slightly further ventrally than the medial, and terminates distal to the articulation between the distal fibula and calcaneum. The distal portion of the tibia does not back the calcaneum, as is the condition

for most tetanuran theropods, but the posterolateral portion of the distal tibia does have a small contact with the dorsomedial corner of the posterior calcaneum (Fig. 19A). The lateral malleolus of the distal tibia is slightly tab-shaped, and similar in morphology to that of *Dilophosaurus wetherilli* (UCMP 77270; 37303). This tab-like process is better developed in *Liliensternus* (MB R.2175), *Zupaysaurus* (Ezcurra & Novas, 2007), and *Piatnitzkysaurus* (PVL 4073). Anteriorly the tibia bears a large distolateral fossa for reception of the ascending process of the astragalus. The fossa is bordered dorsally by a distinct ridge, which extends proximolaterally to distomedially across the anterior face of the distal tibia.

Only the distal portion of the left fibula is preserved in articulation with the distal left tibia and calcaneum (Fig. 19). The distal end of the fibula is moderately expanded anteroposteriorly to about 1.5 times the anteroposterior width of the fibular shaft. Distally, the fibula is slightly convex to match the shallow concave proximal articular surface of the calcaneum. The fibula is closely appressed to the tibia throughout their preserved contact, but distally the fibula bows slightly laterally to accommodate the lateral expansion of the distal tibia. Posteriorly, the distal fibula rests entirely on the dorsal articular surface of the calcaneum, but the anteromedial portion of the distal fibula sits in a shallow fossa on the astragalus lateral to the ascending process.

The left astragalus is preserved in articulation with the calcaneum and distal tibia, but does not appear to be fused to any of these elements (*contra* Hammer & Hickerson, 1994: 829) (Fig. 19). The astragalar condyles are orientated distally, as in all basal theropods. As in most theropods, the astragalar body takes on an hour-glass shape, with the medial side being slightly more robust and longer anteroposteriorly. The

mediolateral width of the astragalus is also slightly greater on the anterior side than on the posterior side. Posteriorly, the medial side of the astragalus is higher dorsoventrally than the lateral side, and contacts only the distal half of the calcaneum. This posterior shape of the astragalus fits the slant of the distal tibia, which has a lateral side that extends further distally than the medial side. The medial end of the astragalus is robust and weakly crescent-shaped, with a convex, semicircular distal surface and a distinct trough proximally to receive the medial portion of the distal tibia. The medial side of the astragalus is flat, with slightly raised rims at its edges.

There is no posteromedial process on the astragalus that caps the posterior part of the medial side of the distal tibia, as in several allosauroids (Allain, 2001). However, a distinct 'knob' is present in a similar position on the posteromedialmost portion of the astragalus. This posteromedial 'knob' is similar in morphology to that of *Torvosaurus* (Britt, 1991), in that it is more robust and distinct than the posteromedial portion of the astragali of basal theropods such as *Ceratosaurus* (YPM 4681) and *Dilophosaurus wetherilli* (UCMP 37302), but is not as well developed as the posteromedial astragalar processes of allosauroids.

The anterior face of the astragalus is partially damaged due to several articulated mid-caudals that had been preserved across it (Fig. 19B, C). There are no distinct foramina on the anterior face of the astragalus, and two shallow, vertical grooves across the middle of the condyles are a result of removing the overlying caudals. Overall, the anterior side of the astragalus bears much resemblance to that of *Dilophosaurus wetherilli* (UCMP 37302). A shallow, horizontal groove is present on the anterior face of the astragalus, and is more pronounced at its medial end (Fig. 19B, C). This groove is not as deeply excavated as in *Ceratosaurus* (YPM 4681) and most tetanurans, but is similar to the morphology present in smaller theropods such as *Dilophosaurus wetherilli* (UCMP 37302), *Masiakasaurus* (Carrano et al., 2002) and '*Syntarsus*' *kayentakatae* (Tykoski, 2005). The ascending process is triangular, with a broad base arising out of the lateral side of the astragalus, and a finger-like dorsal tip (Fig. 19B, C). The ascending process is set back caudally from the anterior face of the astragalar condyles, but there is not a deep anterior fossa at its base as in some tetanurans. The height of the ascending process slightly exceeds the height of the anterior face of the astragalus, as in *Dilophosaurus wetherilli* (UCMP 37302).

The entire left calcaneum is preserved in articulation with the left fibula, tibia and astragalus (Fig. 19). The calcaneum is robust and crescent-shaped, with a highly convex, semicircular distal surface. The proximal surface is only slightly concave, to create a small trough for reception of the distal fibula. The lateral surface is relatively unmarked. It is slightly concave, due to the low raised edges of the calcaneum. The distal rounded edge of the calcaneum appears to be more robust anteriorly. The calcaneum is roughly twice as long anteroposteriorly than wide mediolaterally. It completely covers the distal fibula in posterior aspect, but only articulates with the anterolateral portion of the fibula anteriorly. The posterodorsal corner of the calcaneum is similar to that of basal theropods such as *Dilophosaurus wetherilli* (UCMP 37302), *Torvosaurus* (Britt, 1991: fig. 23) and *Baryonyx* (Charig & Milner, 1997: fig. 43), and does not come to as distinct a point and extend as far proximally as in *Allosaurus* (Madsen, 1976) or *Sinraptor* (Currie & Zhao, 1994a: fig. 23). In posterior aspect, the calcaneum is roughly square, except for the dorsomedial corner, which is slightly rounded and truncated for its small contact with the posterolateralmost portion of the distal tibia, similar to the condition in *Dilophosaurus wetherilli*, *Elaphrosaurus*, *Coelophysis rhodesiensis* and '*Syntarsus*' *kayentakatae* (Tykoski, 2005). In these taxa the tibial–calcaneal articulation is restricted to the dorsomedial corner of the posterior calcaneum, and there does not appear to be a distinct articular facet for the tibia on the calcaneum as in most tetanuran theropods.

PHYLOGENETIC SYSTEMATICS

METHODS

The skeleton of *Cryolophosaurus* possesses several characteristics that diagnose it as a neotheropod, including the presence of: (1) pleurocoels in the cervical vertebrae, and (2) a distal tibia with an expanded lateral process (Rauhut, 2003). *Cryolophosaurus* also lacks most characters considered to be diagnostic of Coelurosauria, including: (1) a round orbit; (2) absence of a lacrimal horn (i.e. a lacrimal horn is present in *Cryolophosaurus*); (3) short, broad cervical ribs; and (4) subrectangular, sheet-like neural spines on the mid-caudal vertebrae (Norell, Clark & Makovicky, 2001; Rauhut, 2003). These observations, coupled with the results of earlier studies (Sereno et al., 1996; Carrano & Sampson, 2003; Smith et al., 2005), suggest that *Cryolophosaurus* is a basal theropod dinosaur. In order to place *Cryolophosaurus* within Theropoda more accurately, a phylogenetic analysis of 56 theropod taxa and 347 characters was undertaken.

Ingroup taxa were selected for the phylogenetic analysis with the primary goal of including multiple representatives of major groups at the base of Theropoda. Several coelurosaur taxa were included in an attempt to provide an accurate and comprehensive representation of character distribution at the node Coelurosauria. Six Triassic dinosauriforms were chosen as outgroup taxa for the analysis: *Silesaurus*,

Marasuchus, *Saturnalia*, *Plateosaurus*, *Herrerasaurus* and *Eoraptor*. The choice of outgroup taxa was designed primarily to provide an accurate assessment of character polarities for the neotheropod node, and should not be viewed as a robust test of basal dinosaur relationships.

Most of the characters utilized in the present analysis are taken from previous works (Gauthier, 1986; Sereno *et al.*, 1994, 1996, 1998; Harris, 1998; Sampson *et al.*, 1998; Tykoski, 1998, 2005; Forster, 1999; Sereno, 1999; Currie & Carpenter, 2000; Holtz, 2000; Allain, 2002; Carrano *et al.*, 2002; Coria & Currie, 2002; Rauhut, 2003; Hwang *et al.*, 2004; Novas *et al.*, 2005; Yates, 2005). Regardless of original authorship, the majority of characters in this analysis were taken from three sources: (1) Carrano *et al.*'s (2002) analysis of basal theropod phylogeny, which focused heavily on neoceratosaurs; (2) Rauhut's (2003) analysis of basal theropod phylogeny, which focused heavily on basal tetanurans; and (3) Norell *et al.*'s (2006) analysis of coelurosaurian relationships (note that this represents one of the more recent incarnations of the Theropod Working Group's character matrix: Norell *et al.*, 2001; Xu *et al.*, 2002; Hwang *et al.*, 2004).

The character list and taxon-character matrix are provided in supplementary Appendixes S1 and S2, respectively. All characters were equally weighted and treated as unordered. A maximum-parsimony analysis was performed on the data matrix using PAUP*4.0b10 (Swofford, 2002). A heuristic search was performed with 25 000 random addition sequence replicates using the tree bisection and reconnection (TBR) branch swapping algorithm. Character-state transformations were evaluated under both ACCTRAN and DELTRAN optimizations. Support for the resulting maximum-parsimony trees (MPTs) was quantified by performing a bootstrap analysis (Felsenstein, 1985). Heuristic searches were performed on 2000 pseudoreplicate data sets, with ten random addition sequence replicates for each search. The maximum number of trees saved for each random addition sequence replicate was set to 100 to prevent the searches from becoming stuck on a large island of MPTs during any particular random addition sequence replicate. This strategy drastically reduces the amount of treespace explored for any given random addition sequence replicate, but it does allow for a relatively large number of bootstrap replicates to be performed. Bremer support values were also calculated for each node in the strict consensus of all MPTs using TreeRot.v2c (Sorenson, 1999).

RESULTS

The analysis resulted in the recovery of 108 MPTs, each of which had a length of 833 steps, a consistency index (CI) of 0.489, a rescaled consistency index (RC) of 0.377 and a retention index (RI) of 0.772. The strict consensus of these MPTs is fairly well resolved (Fig. 20). The Adams consensus tree of all MPTs is identical to the strict consensus. The results of the present phylogenetic analysis support the monophyly of several previously recognized major theropod clades, including: Neoceratosauria, Tetanurae, Spinosauroidea and Coelurosauria (Gauthier, 1986; Rowe, 1989; Rowe & Gauthier, 1990; Holtz, 1994, 2000; Sereno *et al.*, 1994, 1996, 1998; Harris, 1998; Currie & Carpenter, 2000; Allain, 2002; Carrano *et al.*, 2002; Rauhut, 2003; Wilson *et al.*, 2003). Support throughout the strict consensus tree is relatively weak, with the highest levels of support being concentrated within Coelurosauria, Neoceratosauria and also at the Theropoda root (Fig. 20).

One interesting result of the phylogenetic analysis is the recovery of a non-monophyletic Coelophysoidea, with *Zupaysaurus*, *Dilophosaurus wetherilli*, and several other taxa (including *Cryolophosaurus*) recovered as more closely related to neoceratosaurs and tetanurans than to *Coelophysis* (Fig. 20). A basal clade of theropods (referred to here as 'coelophysoidea'), consisting of most traditional coelophysoids (*Liliensternus*, *Coelophysis*, '*Syntarsus*' *kayentakatae* and *Segisaurus*) is supported by five unambiguous synapomorphies, including: elongate cervical centra, an ilium bearing a posterior notch in lateral aspect, an ischium that is less than two-thirds the length of the pubis, and a ventral boss on the proximal end of the third metatarsal. However, a clade composed of *Zupaysaurus* and all other neotheropods constitutes the sister-taxon to this depauperate 'coelophysoidea'. This clade is supported by eight unambiguous synapomorphies: a tooth row that ends at the anterior rim of the orbit, a jugal with an expanded anterior end, the presence of a lacrimal fenestra, a broad contact between the squamosal and quadratojugal, the presence of a well-developed anterior wall to the lateral mandibular glenoid, a broadened retroarticular process, a posterodorsally facing surface for the attachment of the m. depressor mandibulae on the retroarticular process, and an astragalar ascending process that is higher than the astragalar body. *Zupaysaurus* is sister-taxon to a clade that is composed of: (1) a clade of medium-sized Early Jurassic theropods, (2) Neoceratosauria and (3) Tetanurae. This large clade is supported by five unambiguous synapomorphies: the presence of a dorsoventrally elongate orbit, maxillae that are orientated subparallel to each other in dorsal aspect, a reduced maxillary tooth count, a tongue-like process of the parietals overlapping the supraoccipital knob, and a relatively deep surangular. This clade of several medium-sized Early Jurassic theropods includes '*Dilophosaurus*' *sinensis*, *Dracovenator*, *Dilophosaurus wetherilli* and
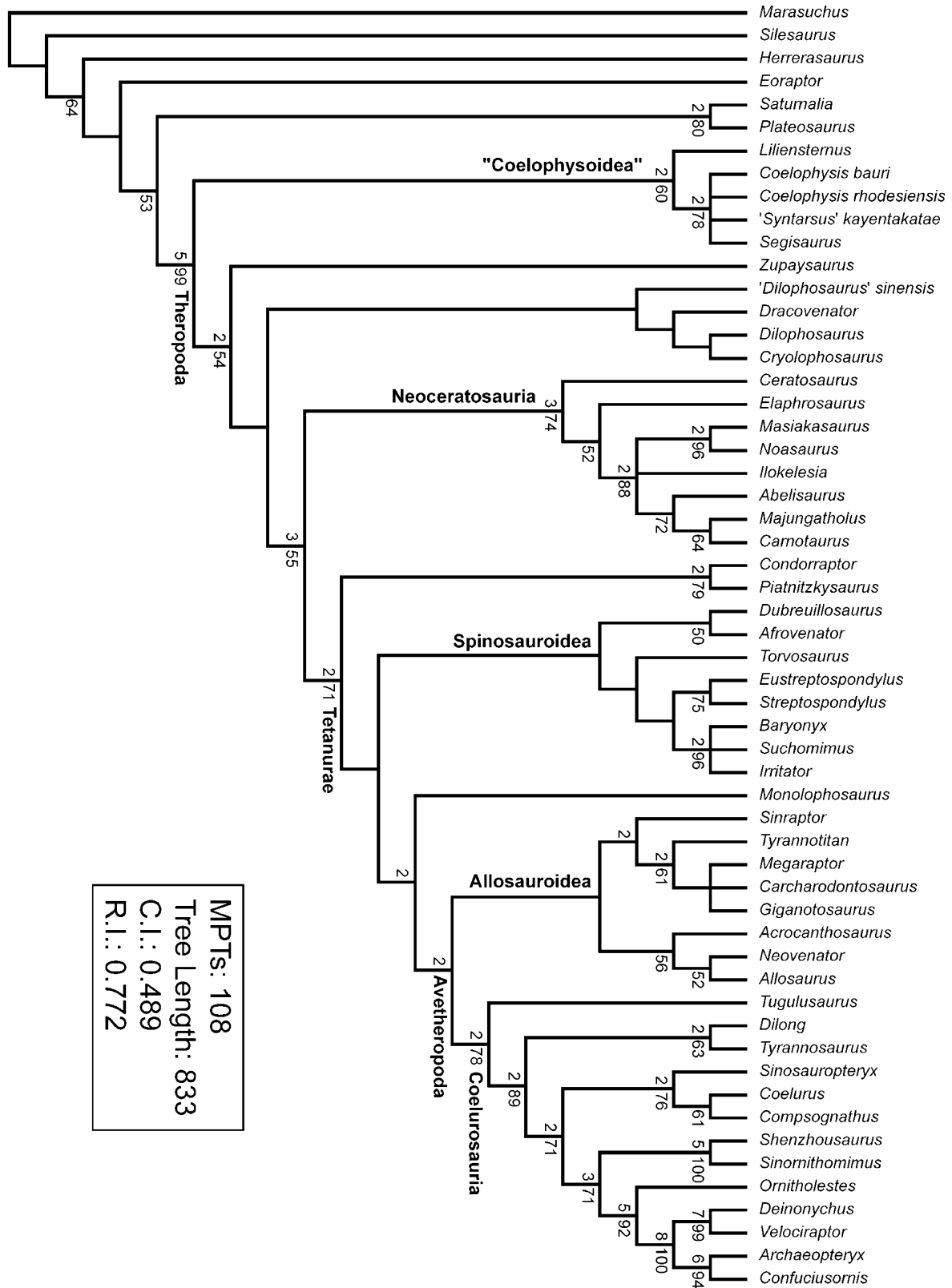
Figure 20. Strict consensus of 108 MPTs. All trees have length of 833 steps, CI 0.489, RI 0.772. Bootstrap values > 50% are listed to the left of nodes, and Bremer support values > 1 are listed to the right. Several theropod clades are indicated in bold.

Cryolophosaurus. Although relationships within this clade are completely resolved in the set of MPTs, support for these relationships, and for monophyly of the clade as a whole, are weak. Three unambiguous synapomorphies diagnose the clade: a contribution of the premaxillary posterodorsal process to a blade-like nasal crest, extension of the antorbital fossa onto the lateroventral side of the nasal and presence of a nasolacrimal crest. Several additional characters that are unknown in one or more of the four taxa may also support this group, including: a slot-shaped foramen on the lateral face of the premaxilla at the base of the nasal process (present in *Dracovenator* and *Dilophosaurus wetherilli*), and the presence of erect, tab-like dorsal processes on the articular (present in *Dracovenator*, *Dilophosaurus wetherilli* and *Cryolophosaurus*). A low height/length ratio of the premaxilla below the external naris constitutes an unambiguous synapomorphy that unites *Dracovenator*, *Dilophosaurus wetherilli* and *Cryolophosaurus* to the exclusion of '*Dilophosaurus*' *sinensis*. *Dilophosaurus wetherilli* and *Cryolophosaurus* are recovered as sister taxa based on the shared presence of a lateral groove along the posterior end of the surangular in both of these taxa.

In contrast to many traditional analyses (Gauthier, 1986; Rowe, 1989; Rowe & Gauthier, 1990; Holtz, 1994, 2000; Sereno *et al.*, 1996; Tykoski, 1998, 2005; Tykoski & Rowe, 2004), but in agreement with a growing number of studies (Rauhut, 2000, 2003; Carrano *et al.*, 2002; Carrano & Sampson, 2003; Wilson *et al.*, 2003; Sereno *et al.*, 2004), Neoceratosauria is recovered as the sister group to Tetanurae. Nineteen characters throughout the skeleton unambiguously support the Neoceratosauria + Tetanurae clade, including: the absence of a quadrate foramen, prezygapophyses that are situated lateral to the neural canal in the anterior cervicals, a scapula that is not markedly expanded at its distal end, a pronounced ventral hook on the anterior portion of the ilium, a broadened 'wing-like' lesser trochanter, a reduced fibular facet on the astragalus, and a plate-like astragalar ascending process.

A Neoceratosauria (*sensu* Carrano *et al.*, 2002; 'Ceratosauria' of Rauhut, 2003) clade is also recovered in the present analysis. *Ceratosaurus* and *Elaphrosaurus* are recovered as successive sister-taxa to a Noasauridae + Abelisauridae clade, as in the analyses of Holtz (1994) and Rauhut (2003; though Rauhut did not recognize the distinction between the two families, and instead placed *Noasaurus* within Abelisauridae). In contrast, Tykoski (1998, 2005), Holtz (2000), Carrano *et al.* (2002), Wilson *et al.* (2003), Sereno *et al.* (2004) and Tykoski & Rowe (2004) recovered the opposite arrangement, with *Elaphrosaurus* representing the basal-most neoceratosaur, and *Ceratosaurus* recovered as sister-taxon to a Noasauridae + Abelisauridae clade. Tykoski (2005) suggested that one explanation for the

basal position recovered for *Elaphrosaurus* in his analysis could be due to the many similarities this taxon shares with coelophysoids. The sister-taxon relationship between *Elaphrosaurus* and a Noasauridae + Abelisauridae clade is well supported in the analysis of Rauhut (2003; recovered in 92% of bootstrap replicates), but only weakly so in the present analysis (recovered in 52% of bootstrap replicates, and a Bremer support value of 1). Within Neoceratosauria, the results of the present phylogenetic analysis support the previously recognized monophyly of Abelisauroidea and its two families, Noasauridae and Abelisauridae (Carrano *et al.*, 2002; Wilson *et al.*, 2003; Tykoski & Rowe, 2004; Tyksoki, 2005).

The clade Tetanurae is also recovered in the present analysis, and is supported by 14 unambiguous synapomorphies, including: a pneumatic excavation/antrum in the maxillary anterior ramus, pneumatic openings associated with the internal carotid artery, a rod-like axial neural spine, robust ventral keels in the anterior dorsal vertebrae, a horizontally directed femoral head, a fibular condyle on the tibia that is strongly offset from the tibial cnemial crest, a distally placed fibular ridge on the tibia, a metatarsal III with an hourglass-shaped proximal outline and a metatarsal IV with a well-developed posteromedial flange. Interestingly, *Condorraptor* and *Piatnitzkysaurus* are recovered in a sister-taxa relationship at the base of Tetanurae, in contrast to Rauhut's (2005a) claim that the two are unrelated stem tetanurans. Several characteristics originally described in *Condorraptor* (i.e., a low ridge running across the base of the transverse process of the first sacral vertebrae, step-like lateral ridges on the hyposphenes of the posterior dorsal vertebrae) are also present in *Piatnitzkysaurus* (PVL 4073; MACN CH 895).

Within Tetanurae, Spinosauroidea, *Monolophosaurus* and Allosauroidea represent successive sister-taxa to Coelurosauria. A (Spinosauroidea + *Monolophosaurus* + Avetheropoda) clade is supported by six unambiguous synapomorphies including: a long anterior projection of the maxillary body that is offset from the ascending ramus of the maxilla, parapophyses that are placed below the transverse process in the posterior dorsals, an ischial peduncle that tapers ventrally and lacks a well-defined articular facet, and a medially directed femoral head. This result is similar to most studies (Sereno *et al.*, 1994, 1996; Allain, 2002; Carrano *et al.*, 2002; Holtz, Molnar & Currie, 2004), but differs from those of Holtz (1994, 2000), and Charig & Milner (1997; using a taxon-character matrix modified from Holtz, 1994) in recognizing a monophyletic, rather than paraphyletic, Spinosauroidea. This result also differs from that of Rauhut's (2003) study, which recovered a monophyletic Carnosauria (Spinosauroidea + Allosauroidea) as sister-

taxon to Coelurosauria, though only three additional steps in Rauhut's (2003) tree are required to obtain the relationship proposed here (Rauhut, 2003: 167).

Though a monophyletic Spinosauroidea is only weakly supported by bootstrap and Bremer support values, five unambiguous synapomorphies diagnose the clade: a long premaxillary body in front of the external nares, a lacrimal lateral blade that does not overhang the antorbital fenestra, a postorbital with a U-shaped ventral process, a reduced participation of the supraoccipital in the dorsal margin of the foramen magnum and a brevis fossa with a shallow lateral wall. There is limited resolution within Spinosauroidea, though a spinosaurid (*sensu* Sereno *et al.*, 1998) clade is relatively well supported. Interestingly, a group consisting of *Eustreptospondylus* and *Streptospondylus altdorfensis* is recovered as sister-taxon to this clade. This relationship is supported by four unambiguous synapomorphies, including: a dentary with an anterior end that is expanded and bears enlarged fang-like teeth, and an obturator foramen in the pubis that is open ventrally. *Eustreptospondylus* and *Streptospondylus altdorfensis* are united by the absence of a strong ventral keel in the anterior dorsals, and the presence of paired hypapophyses on the anterior dorsals. Despite the presence of structure within Spinosauroidea recovered in this, and previous analyses (Sereno *et al.*, 1998; Allain, 2002), the ongoing revision of the European 'megalosaurid' record will be critical to establishing robust hypotheses of relationship within this clade (Allain, 2001, 2002, 2005; Allain & Chure, 2002; Day & Barrett, 2004; Sadleir, 2004; Sadleir, Barrett & Powell, 2004).

Relationships within Allosauroidea are well resolved in the current analysis, though some are weakly supported. In contrast to several analyses, the Middle Jurassic *Monolophosaurus* is recovered as sister taxon to Avetheropoda, rather than as the most basal allosauroid (Currie & Carpenter, 2000; Holtz, 2000; Rauhut, 2003; Novas *et al.*, 2005). The clade Allosauroidea is supported by four unambiguous synapomorphies, including: paroccipital processes that are directed strongly ventrolaterally, subdivided basal tubera and a well-defined posteromedial process on the astragalus (also present in *Fukuiraptor*, Azuma & Currie, 2000; *Mapusaurus*, Coria & Currie, 2006). In contrast to the analyses of Holtz (2000), and Novas *et al.* (2005), but in agreement with several recent analyses (Allain, 2002; Coria & Currie, 2002; Rauhut, 2003), a sister-group relationship between *Sinraptor* and Carcharodontosauridae is recovered. Five unambiguous synapomorphies support the sister-group relationship of *Sinraptor* and Carcharodontosauridae, including several characters of the braincase discussed in more detail in Coria & Currie (2002), but also the presence of an anterior spur on the jugal pro-

cess of the postorbital, and the absence of pneumatic openings associated with the internal carotid artery. A carcharodontosaurid clade is supported by five unambiguous synapomorphies, although many other characters may also support this clade, but are only optimized as such under accelerated transformation character optimization (ACCTRAN), due to the fragmentary nature of the basal-most carcharodontosaurid, *Tyrannotitan*. Interestingly, the enigmatic theropod *Megaraptor* is recovered as a carcharodontosaurid. This relationship is primarily supported by several characters of the cervical vertebrae, including the number and orientation of cervical pleurocoels, and the presence of a marked prezygapophyseal–epipophyseal lamina (Calvo *et al.*, 2004a). *Megaraptor* also shares with several carcharodontosaurids the presence of hyposphene/hypantrum-like accessory articulations in the cervical vertebrae, and the presence of pleurocoels in the caudal vertebrae. An allosaurid clade is recovered as sister-group to the *Sinraptor* + Carcharodontosauridae clade. This clade includes *Allosaurus*, the unusual European taxon *Neovenator* and also *Acrocanthosaurus*, in contrast to several studies that have placed this taxon within Carcharodontosauridae (Sereno *et al.*, 1996; Holtz, 2000; Holtz *et al.*, 2004). Four unambiguous synapomorphies diagnose Allosauridae: the absence of a basioccipital participation in the basal tubera, complete separation of the ophthalmic branch of the trigeminal nerve, a distinct 'kink' along the anterior margin of the neural spines of the anterior to mid-caudal vertebrae, and the presence of an anterior spur in front of the neural spine of the mid-caudal vertebrae (though the first two characters are unknown in *Neovenator*). However, the presence of a separate opening for the ophthalmic branch of the trigeminal nerve may diagnose a more inclusive clade, as this character is also present in *Tyrannosaurus*, *Troodon* and most birds (Currie & Zhao, 1994b: 2239). A separate opening for the ophthalmic branch also occurs in crocodylomorphs (Wu & Chatterjee, 1993; Currie & Zhao, 1994b: 2239), though this is almost certainly the result of convergence. The presence of anterior spurs on the mid-caudal neural spines is also slightly homoplastic, being present in several spinosauroids (e.g., *Dubreuillosaurus*, *Poekilopleuron*), and the basal coelurosaurs *Compsognathus* and *Sinosauropteryx* (Allain & Chure, 2002; Rauhut, 2003; Allain, 2005). *Allosaurus* and *Neovenator* are united in a clade based on the shared presence of five maxillary teeth, and an anterior ramus of the maxillary body that is as long as high, or longer.

Weak support for Avetheropoda (= Allosauroidea + Coelurosauria) is probably due to the recovery of *Monolophosaurus* as sister taxon to this clade, thus dividing support for a traditional Allosauroidea (including *Monolophosaurus*) + Coelurosauria clade

across two nodes (Brochu, 1997; Shaffer, Meylan & McKnight, 1997). A (*Monolophosaurus* + Avetheropoda) clade is supported by five unambiguous synapomorphies, including: associated frontals that are as wide as long, an anteroposteriorly broad dorsal process of the quadratojugal, a large quadrate foramen present between the quadrate and quadratojugal, and basal tubera that are less than the width of the occipital condyle. Avetheropoda is supported by eight unambiguous synapomorphies that include: the presence of a maxillary fenestra that penetrates the medial wall of the maxilla, a short lacrimal anterior ramus, reduction of the width of the ventral ramus of the lacrimal, axial pleurocoels, and an ischial obturator process that is offset from the pubic peduncle by a distinct notch.

The basal nodes of Coelurosauria are among the most well supported in the current analysis. *Tugulusaurus* is recovered as the basal-most coelurosaur, in accordance with a recent reanalysis of this taxon by Rauhut & Xu (2005). Although relationships within Coelurosauria are well resolved and highly supported in the present analysis, part of this can be attributed to the limited taxon sampling within this clade. Taxon sampling within Coelurosauria was undertaken along the same lines as outlined in the 'methods' section above, but was limited in scope, as the primary goal of including coelurosaur taxa was to provide accurate reconstructions of character states at the node Coelurosauria, and not necessarily to resolve relationships within Coelurosauria. For these reasons, support for various coelurosaurian clades in the present analysis will not be discussed in detail (and the above note on taxon sampling should be considered when interpreting support values for coelurosaurian clades from the present analysis). It should be sufficient to note that several major, and relatively uncontroversial, clades within Coelurosauria are recovered in the present analysis, including Tyrannosauroidea, Coeluridae (= 'Compsognathidae'), Ornithomimosauria, Paraves, Deinonychosauria/ Dromaeosauridae (no troodontids were included in the present analysis, so support for these two nested clades is not divided on the branch leading to *Deinonychus* + *Velociraptor*), and Avialae.

DISCUSSION

PHYLOGENETIC RELATIONSHIPS AND IMPLICATIONS

Several interesting results of the present analysis include the recovery of: (1) a non-monophyletic Coelophysoidea, (2) a clade of medium-bodied, Early Jurassic theropods that includes *Cryolophosaurus*, (3) a sister-taxon relationship between *Piatnitzkysaurus* and *Condorraptor*, (4) the Late Cretaceous taxon *Megaraptor* as a carcharodontosaurid, and (5) a sister-taxon relationship between *Monolophosaurus* and an Allosauroid + Coelurosauria clade.

Several previous studies have suggested Coelophysoidea may be non-monophyletic (Carrano *et al.*, 2002; Rauhut, 2003; Yates, 2005), and the results presented here provide additional support for this hypothesis. Interestingly, doubts regarding the 'coelophysoid' affinities of all of the taxa recovered as more closely related to derived neotheropods have been presented before (Hammer & Hickerson, 1994; Lamanna *et al.*, 1998; Carrano *et al.*, 2002; Arcucci & Coria, 2003; Rauhut, 2003; Yates, 2005). Part of the recovery of a non-monophyletic Coelophysoidea in the present analysis can be attributed to the inclusion of several taxa (e.g. *Dracovenator*, '*Dilophosaurus*' *sinensis*, *Cryolophosaurus*) that possess a mosaic of 'coelophysoid' and more derived theropod characters. However, this result is also due to our hypothesis of a broader distribution of many traditional 'coelophysoid' characters. For example, the presence of reduced or absent axial parapophyses and diapophyses have been considered synapomorphies of Coelophysoidea by several authors (Rowe, 1989; Tykoski & Rowe, 2004; Tykoski, 2005). However, reduced axial parapophyses are also present in *Piatnitzkysaurus* (PVL 4073), and reduced axial diapophyses are also present in *Piatnitzkysaurus* (PVL 4073), *Silesaurus* (Dzik, 2003), and possibly *Herrerasaurus* (Carrano *et al.*, 2005). Several basal saurischians and basal sauropodomorphs also apparently lack marked diapophyses (O. Rauhut, pers. comm. 2006). A kinked articular facet of the iliac pubic peduncle has also been suggested as a 'coelophysoid' synapomorphy (Tykoski & Rowe, 2004; Tykoski, 2005). This morphology appears to be more widely distributed as well, being present in the tetanuran *Monolophosaurus* (IVPP 84019), and the dinosauriforms *Marasuchus* (PVL 3871), *Silesaurus* (Dzik, 2003) and *Herrerasaurus* (PVL 2566). The presence of a tab-like tibial lateral malleous is another example of a character that has been considered a synapomorphy of Coelophysoidea (Sereno, 1999; Carrano *et al.*, 2005), but appears to be more widely distributed. *Elaphrosaurus* (MB dd unnumbered holotype), *Ceratosaurus* (YPM 4681), *Piatnitzkysaurus* (PVL 4073) and *Sinraptor* (Currie & Zhao, 1994a) all possess distal tibiae with tab-like lateral borders. Despite the recovery of a non-monophyletic Coelophysoidea in the MPTs from the present analysis, support for this non-traditional topology is relatively weak, with low bootstrap and Bremer decay values recovered for the nodes separating *Zupaysaurus* and the several Early Jurassic taxa from 'coelophysoids' (Fig. 20). Constraining *Zupaysaurus* to group with the five basal-most 'coelophysoid' neotheropods results in a topology that is no more than five steps longer than the 833 steps in the MPTs recovered here. Constraining both *Zupaysaurus* and

Dilophosaurus wetherilli to group with these five 'coelophysoids' results in a topology that is no more than six steps longer than the MPTs, and also groups the additional taxa *Dracovenator*, '*Dilophosaurus*' *sinensis* and *Cryolophosaurus* within a monophyletic Coelophysoidea. Thus, support for the non-monophyly of a traditional Coelophysoidea should currently be regarded as tentative (Carrano *et al.*, 2002; Rauhut, 2003; Yates, 2005). However, our results suggest that improved character and taxon sampling of the Early– Mid Jurassic theropod record offers the potential to shed more light on this issue.

Another interesting result related to the recovery of a non-monophyletic Coelophysoidea in the present analysis is the recovery of a clade of medium-bodied Early Jurassic theropods. This clade is composed of '*Dilophosaurus*' *sinensis*, *Dracovenator*, *Dilophosaurus wetherilli* and *Cryolophosaurus*, and constitutes the sister-taxon to a (Neoceratosauria + Tetanurae) clade (Fig. 20). All four taxa are very similar in size, with estimates of skull length and overall body length varying from 500 to 700 mm and 5.5 to 6.5 m, respectively. Interestingly, with the exception of *Cryolophosaurus*, which is known from the relatively unexplored Hanson Formation, all of these taxa are known from formations or biostratigraphic intervals that also preserve smaller-bodied 'coelophysoids' that are not closely related to them. '*Dilophosaurus*' *sinensis* and a fragmentary specimen referred to *Megapnosaurus* (= '*Syntarsus*') are known from the Lower Lufeng Formation of China (Hu, 1993; Irmis, 2004). *Dracovenator* is known from the upper Elliot Formation, which may be correlative with the Forest Sandstone Formation from which *Coelophysis rhodesiensis* is known (Olsen & Galton, 1984; Bristowe & Raath, 2004; Yates, 2005). Regardless of the exact correlation of the two formations, both are within the *Massospondylus* Range-Zone of southern Africa (Kitching & Raath, 1984; Yates, 2005). Finally, both *Dilophosaurus wetherilli* and '*Syntarsus*' *kayentakatae* are known from the Kayenta Formation of the south-western United States. An additional 'coelophysoid' taxon is also known from the Kayenta Formation and is smaller in size than both *Dilophosaurus wetherilli* and '*Syntarsus*' *kayentakatae* (Tykoski, 1998; Tykoski & Rowe, 2004). Although the recovery of a non-monophyletic Coelophysoidea, and a clade of medium-bodied Early Jurassic theropods recovered as sister taxon to Neoceratosauria + Tetanurae, does not negate the hypothesis that small size was a derived trait for at least several 'coelophysoid' taxa [e.g. *Segisaurus*, unnamed taxon from the Kayenta Formation (Tykoski, 1998; Tykoski & Rowe, 2004; Carrano *et al.*, 2005)], the topology recovered here may suggest that the ancestral body size at the root of Neotheropoda was smaller than has been recently suggested (Carrano *et al.*, 2005).

The analysis conducted here also represents the first rigorous phylogenetic analysis of the relationships of *Condorraptor currumili*, a purported basal tetanuran from the Cañadón Asfalto Formation of Argentina (Rauhut, 2005a). A sister-taxon relationship between *Condorraptor* and *Piatnitzkysaurus*, also from the Cañadón Asfalto Formation, is supported in the present analysis by two unambiguous synapomorphies: the presence of a low, robust ridge running across the base of the transverse process of the first sacral vertebra, and the presence of step-like ridges lateral to the hyposphenes in the dorsal vertebrae. The sacral ridges of both *Piatnitzkysaurus* (MACN 895) and *Condorraptor* (MPEF-PV 1701) begin at the anterior border of the transverse process, near its base and the base of the prezygapophysis. The sacral ridge rises dorsally and curls posteromedially across the dorsal surface of the base of the transverse process in both taxa. The posteriormost portion of the right and left sacral ridge of *Piatnitzkysaurus* (MACN 895) is not completely preserved, but it is clear that the ridges are not as high dorsally as they are in *Condorraptor* (MPEF-PV 1701). The step-like lateral ridges to the hyposphene are much more prominent in the posterior dorsal vertebrae of *Piatnitzkysaurus* (PVL 4073). This structure begins posteriorly as a small, conical ridge at the lateroventral corner of the hyposphene and the dorsal border of the neural canal. This conical ridge possesses a rugose, dorsomedially facing surface that articulates with a ventral flange extending from the medial edge of the prezygapophysis of the proceeding vertebra. Thus, the step-like ridges probably represent accessory vertebral articulations. The conical ridge sweeps anterodorsally as a low, laminar ridge to connect with the posterior edge of the articular facet of the postzygapophysis. The surface of the bone of this laminar ridge is much smoother than the conical portion of the structure, and is similar in texture to the surface of the infrapostzygapophyseal fossa. In more anterior dorsal vertebrae of *Piatnitzkysaurus* (PVL 4073), the step-like lateral ridges are much smaller and more medially placed, being more or less attached to the anterolateral border of the hyposphene. The variation in prominence of this structure throughout the dorsal vertebrae, and the subtleness of its morphology to begin with, suggests that caution should be used when assessing the distribution of this structure across theropod taxa. An additional feature that may suggest a close relationship between *Condorraptor* and *Piatntizkysaurus* is the presence of a low ridge on the lateral side of the tibial cnemial crest that bounds a depression at the distal base of the cnemial crest (Rauhut, 2005a). This feature was originally considered an autapomorphy of *Condorraptor* by Rauhut (2005a), but a similar ridge and associated fossa is present in *Piatnitzkysaurus*

(MACN 895; this area of the tibia is damaged in PVL 4073, but a faint portion of the ridge and fossa still appear to be visible). In *Piatnitzkysaurus* (MACN 895) this ridge is more proximally placed than in *Condorraptor* (MPEF-PV 1672), and extends posterodistally from the anteroproximal corner of the lateral side of the cnemial crest. The recovery of *Condorraptor* as sister-taxon to *Piatnitzkysaurus* is important as it suggests that although tetanuran diversification in the Middle Jurassic was global, at least some endemicity was present at lower taxonomic levels during this time (Rauhut, 2005a). The sister-taxon relationship recovered between *Eustreptospondylus* and *Streptospondylus*, both from the Callovian–Oxfordian of Europe, also supports this claim (Fig. 20).

In addition to addressing the relationships of *Condorraptor*, the analysis presented here is the first rigorous test of the phylogenetic relationships of the enigmatic *Megaraptor namunhuaiquii*, from the Late Cretaceous of Argentina (Novas, 1998; Calvo *et al*., 2004a). Originally described from fragmentary remains, *Megaraptor* was tentatively referred to the derived theropod clade Coelurosauria (Novas, 1998). Additional material described by Calvo *et al*. (2004a) allowed for the clarification of some aspects of this taxon's anatomy (e.g., that the large, trenchant unguals actually belong to the manus), and these authors suggested that *Megaraptor* probably represented a basal tetanuran, with possible affinities to carcharodontosaurids or spinosaurids. *Megaraptor* is recovered as a derived carcharodontosaurid in the present analysis, being more closely related to *Giganotosaurus* and *Carcharodontosaurus* than to the basalmost carcharodontosaurid, *Tyrannotitan*. Despite this result, *Megaraptor* still possesses several features that suggest spinosauroid affinities (Calvo *et al*., 2004a). Most notable among these is the presence of a large, trenchant manual ungual on the first digit, which is also present in the spinosauroids *Torvosaurus*, *Baryonyx* and *Suchomimus*, and also the coelurosaur *Sinosauropteryx*. Constraining *Megaraptor* to group within a monophyletic Spinosauroidea results in trees that are no more than two steps longer than the MPTs recovered in the present analysis, suggesting that the placement of *Megaraptor* within Carcharodontosauridae should be viewed as tentative. Regardless of whether *Megaraptor* represents a carcharodontosaurid or a spinosauroid, its phylogenetic placement has important implications for faunal change within theropod communities in the early Late Cretaceous. If the Portezuelo Formation is Turonian in age (Leanza, 1999; Calvo *et al*., 2004a), this would make *Megaraptor* the youngest known member of either Carcharodontosauridae or Spinosauroidea. Novas *et al*. (2005) noted that Gondwanan theropod communities were primarily composed of carcharodontosaurids and spinosaurids from the Aptian through the Cenomanian. These authors suggested that after the end of the Cenomanian these assemblages gave way to a radiation of relatively smaller abelisauroids and coelurosaurs (Novas *et al*., 2005). Although Novas *et al*. (2005) also noted that the initial abelisauroid diversification was well underway by the end of the Early Cretaceous, the recovery of the Turonian *Megaraptor* as a carcharodontosaurid, in addition to recent discoveries of early Late Cretaceous abelisauroids (Calvo, Rubilar-Rogers & Moreno, 2004b; Coria, Currie & Carabajal, 2006), significantly increases the overlap between these seemingly disparate 'Middle' and 'Late' Cretaceous Gondwanan theropod faunas.

A final interesting result of the present phylogenetic analysis concerns the recovery of *Monolophosaurus* outside of both Allosauroidea and Avetheropoda, in a more basal position than most previous analyses (Sereno *et al*., 1996; Sereno, 1999; Holtz, 2000; Rauhut, 2003; Holtz *et al*., 2004). The mosaic of plesiomorphic and derived characters present in *Monolophosaurus* has been noted previously (Zhao & Currie, 1994). The result obtained here can primarily be attributed to increased taxon and character sampling across the theropod tree, i.e. many characters previously considered to be synapomorphies of a monophyletic Allosauroidea, such as the presence of a pneumatic foramen in the nasal, the extension of the antorbital fossa onto the lateroventral side of the nasal, a broad contact between the squamosal and quadratojugal, pneumatism associated with the opening for the internal carotid artery, and the presence of a pendant medial process on the articular (Holtz, 1994; Sereno *et al*., 1996), are more widely distributed across theropod taxa. *Monolophosaurus* also possesses several characters that may be synapomorphies of less inclusive clades that are more basal than Avetheropoda, including a ventrally extended postorbital (present in several spinosauroids), a nasolacrimal cranial crest (present as parasagittal structures in several members of the '*Dilophosaurus*' clade; though also present in *Dilong*), a laterally exposed quadratojugal–quadrate suture that forms a sharp lateral flange (present in members of the '*Dilophosaurus*' clade, *Zupaysaurus* and *Irritator*), and a 'kinked' iliac pubic peduncle (present in *Dilophosaurus wetherilli*, 'coelophysoids' and several basal dinosauriforms). Constraining *Monolophosaurus* to group within a monophyletic Allosauroidea results in topologies that are no more than seven steps longer than the MPTs from the phylogenetic analysis. Interestingly, constraining *Monolophosaurus* to group within a monophyletic Spinosauroidea, or outside of a monophyletic (Spinosauroidea + Avetheropoda), results in topologies that are no more than five steps longer than the MPTs, and constraining *Monolophosaurus* to group outside of a

monophyletic Tetanurae requires six additional steps, suggesting that a basal postion within Theropoda, as opposed to allosauroid affinities, is a more plausible hypothesis for the relationships of *Monolophosaurus* given the present phylogenetic data set. Future sampling of the early Middle Jurassic theropod record, and more accurate optimization of the synapomorphies of many theropod clades (e.g. Spinosauroidea, Allosauroidea, Avetheropoda), will aid in further resolving the phylogenetic relationships of this enigmatic taxon.

COMPARATIVE ANATOMY AND PALAEOBIOLOGY OF *CRYOLOPHOSAURUS*

At an estimated weight of 465 kg, *Cryolophosaurus* represents the largest known Early Jurassic theropod (Anderson, Hall-Martin & Russell, 1985). Based on femoral length, *Cryolophosaurus* rivals the largest known specimens of *Ceratosaurus* in size (Madsen & Welles, 2000; Carrano, 2005). Although the neurocentral sutures of all recovered vertebrae (including all regions throughout the axial column: cervical, dorsal, sacral, caudal) of *Cryolophosaurus* (FMNH PR1821) are closed, the fifth sacral (= 'caudosacral 1') lacks any sign of fusion of its centrum to the preceding sacral centrum, and the neurocentral sutures on several of the caudal vertebrae are not obliterated, suggesting that this specimen may not represent a fully mature individual (Brochu, 1996; Irmis, 2007). More specific inferences regarding the ontogenetic stage of *Cryolophosaurus* based on patterns of neurocentral suture closure would be tenuous at best, and await integration with histological data (see discussion in Irmis, 2007). Evidence for a significant increase in theropod body size is present almost immediately after the Triassic–Jurassic transition (Olsen *et al.*, 2002), though these '*Dilophosaurus*'-sized animals would have still been considerably smaller than many of their Late Jurassic relatives (e.g. *Ceratosaurus*, *Allosaurus*). The size of *Cryolophosaurus* suggests that by the end of the Early Jurassic, one or more lineages of theropods had already attained the large size characterized by much of the group's later evolutionary history.

In addition to its large size, *Cryolophosaurus* differs from many early theropods in a variety of features throughout its skeleton. The presence of a dorsoventrally high, furrowed transverse cranial crest in *Cryolophosaurus* is unique among all theropods. However, the construction of this crest, formed by dorsal expansions of the lacrimals which pinch the nasals medially, is similar to the morphology of the posterior portion of the nasolacrimal crests of the Jurassic theropods *Dilophosaurus wetherilli* (UCMP 77270), '*Dilophosaurus*' *sinensis* (Hu, 1993) and *Monolophosaurus* (IVPP 84019). As stated previously (Hammer, 1997), the crest of *Cryolophosaurus* could probably not have functioned in any type of combative role. The diversity of cranial crests present in theropod dinosaurs, including low parasagittal nasal crests ('*Syntarsus*' *kayentakatae*), large blade-like parasagittal nasolacrimal crests (*Dilophosaurus wetherilli*; '*Dilophosaurus*' *sinensis*), pneumatically excavated crests ('*Dilophosaurus*' *sinensis*, *Monolophosaurus*, *Guanlong*), nasal horns (*Ceratosaurus*, several spinosaurids, *Proceratosaurus*) and frontal horns (*Carnotaurus*, *Majungatholus*), tempts speculation that these structures may be associated with sexual dimorphism, or function in species recognition. The amount of data that must truly be marshalled to support these hypotheses (which often represent population-level processes) remains extremely limited for theropods, however, and we support a view that cautions against over-interpreting the available observational data (Padian, Horner & Lee, 2005). Regardless, the phylogenetic distribution of cranial crests suggests that cranial ornamentation may have been ubiquitous throughout theropod evolutionary history. Optimizing the presence of nasal crests on the MPTs recovered in the phylogenetic analysis suggests that some type of nasal crest may have been ancestral for Theropoda.

Another unique feature of *Cryolophosaurus* is the constriction of the infratemporal fenestra by the ventral ramus of the squamosal and the expanded dorsal ramus of the jugal (Fig. 8). Although these elements are not fused, and part of the constriction may be attributed to distortion of the posterior portion of the skull, the constriction of the infratemporal fenestra in *Cryolophosaurus* is more extreme (particularly with regard to the posterodorsally expanded dorsal ramus of the jugal) than in other basal theropods where this constriction is present [e.g. '*Syntarsus*' *kayentakatae* (Rowe, 1989; Tykoski, 1998); *Zupaysaurus* (Arcucci & Coria, 2003); *Dilophosaurus wetherilli* [UCMP 37302]; '*Dilophosaurus*' *sinensis* (Hu, 1993)]. The deeply excavated, dorsoventrally low and anteroposteriorly elongate infradiapophyseal fossae of the posterior cervical vertebrae of *Cryolophosaurus* is also a unique feature among theropods (Fig. 11). However, this morphology is reminiscent of the broadened infradiapophyseal fossae of the cervicals of the poorly known Middle Jurassic Chinese theropod *Chuandongocoelurus* (He, 1984), though the cervical centra of this taxon are also elongated relative to *Cryolophosaurus*. The slender, elongate cranial processes of the cervical ribs represent an additional apomorphic feature of *Cryolophosaurus* (Fig. 11). Several other basal theropods possess elongate cranial processes of the cervical ribs, including *Coelophysis rhodesiensis* (Raath, 1977), '*Syntarsus*' *kayentakatae* and *Spinostropheus* (FMNH cast of MNN TIG6), though in these taxa the cranial processes protrude at most several centimetres past the anterior articular facets of their respective vertebrae,

unlike the extremely elongate condition present in *Cryolophosaurus*. It is notable that the theropod taxa with similar elongated cranial processes on their cervical ribs appear to bracket *Cryolophosaurus* phylogenetically (Fig. 20), provided that *Spinostropheus* represents a basal neoceratosaur (Sereno *et al.*, 2004). Future assessment of the distribution of these structures (which appear to be very fragile, and often incompletely preserved in many theropod specimens) may provide additional insight into the relationships of *Cryolophosaurus*.

Based on the results of the phylogenetic analysis, *Cryolophosaurus* is recovered as being closely related to the Early Jurassic theropods '*Dilophosaurus*' *sinensis*, *Dracovenator* and *Dilophosaurus wetherilli* (Fig. 20), and thus a brief discussion of the features distinguishing *Cryolophosaurus* from these taxa is warranted. *Cryolophosaurus* differs from *Dracovenator* (Yates, 2005) and *Dilophosaurus wetherilli* (UCMP 37302; 77270) in possessing a dorsally facing attachment for the m. depressor mandibulae on the retroarticular process. The dorsal ramus of the quadratojugal is also broader anteroposteriorly in *Cryolophosaurus* than in either *Dilophosaurus wetherilli* (UCMP 37302) or '*Dilophosaurus*' *sinensis* (Hu, 1993). In the axial column, *Cryolophosaurus* lacks the well-rimmed posterior pleurocoels present in the posterior cervicals of *Dilophosaurus wetherilli* (UCMP 77270). The sharp lateral ridge extending from behind the parapophysis in the posterior cervical vertebrae of *Cryolophosaurus* is not present in *Dilophosaurus wetherilli* (UCMP 77270). The transverse processes of the fifth sacral (= 'caudosacral 1') vertebra of *Cryolophosaurus* do not extend as far posteriorly as they do in *Dilophosaurus wetherilli* (UCMP 37302). Many similarities between *Cryolophosaurus* and *Dilophosaurus wetherilli* are present in the appendicular skeleton. However, *Cryolophosaurus* lacks the distinct 'kink' along the dorsal margin of the iliac blade that is present in *Dilophosaurus wetherilli* (UCMP 37302, 77270; Tykoski, 2005), and the supraacetabular shelf of *Cryolophosaurus* does not extend as far posteriorly as in *Dilophosaurus wetherilli* (UCMP 37302). The ischium of *Cryolophosaurus* is also more robust than in *Dilophosaurus wetherilli* (UCMP 37302; Tykoski, 2005), and bears a prominent ischial rugosity. A trochanteric shelf on the proximal femur is present (though partially damaged) in *Crylophosaurus*, and has not been reported in *Dilophosaurus wetherilli*, though this may be due to the relative immaturity of specimens collected to date (Tykoski, 2005). The tarsus of *Cryolophosaurus* and *Dilophosaurus wetherilli* (UCMP 37302, 37303, 77270) are also very similar, with the exception of a small fibular splint located dorsal to the ascending process of the astragalus, although this may be a pathological feature of *Cryolophosaurus*. In summary, many of the specialized and/or unique morphological features of *Cryolophosaurus* appear to be concentrated in the cranial skeleton, suggesting that much of the postcranial anatomy of *Cryolophosaurus* retained a generalized, basal theropod form.

CONCLUSIONS

The theropod dinosaur *Cryolophosaurus* from the Early Jurassic Hanson Formation of Antarctica is important for our understanding of basal theropod evolution for a variety of reasons, but primarily because: (1) it is phylogenetically located in a poorly understood part of the theropod tree, (2) it is from a period of time that is poorly sampled with respect to theropods, and (3) it is from a geographical area, Antarctica, that is poorly sampled for theropods. The present study documents the morphology of *Cryolophosaurus* in detail, and confirms that its suite of plesiomorphic and derived characters place it phylogenetically within a clade of medium-bodied Early Jurassic theropods (including '*Dilophosaurus*' *sinensis*, *Dracovenator* and *Dilophosaurus wetherilli*), that represents the sister taxon to a Neoceratosauria + Tetanurae clade. Thus, a traditional monophyletic Coelophysoidea is not recovered, and a more 'ladder'-like arrangement for basal theropod phylogeny is proposed. However, many of these relationships will remain contentious until the affinities of many early Middle Jurassic theropods from China, and the European 'megalosaurids' are worked out, and until the relationships of basal dinosaur taxa outside of Theropoda are more firmly established. Although *Cryolophosaurus* and the results of the present study provide considerable insight into the evolutionary history of basal theropod dinosaurs, the discovery of more specimens from the early Middle Jurassic (e.g. Rauhut, 2005a; Xu & Clark, 2006), and continued fieldwork in geographical areas and formations that have traditionally been poorly sampled, such as the Hanson Formation of Antarctica, will aid in refining these results. This future work, coupled with rigorous, tree-based analyses of patterns of biogeography, diversification and extinction, will provide the best means to further our knowledge of basal theropod dinosaur evolution.

NOTE ADDED IN PROOF

Further study of the postcranial material of *Cryolophosaurus* has revealed that the fragmentary element tentatively identified as the proximal left tibia (see Fig. 18) actually represents a proximal fragment of the right humerus. This element is missing most of its lateral portion, including the deltopectoral crest, and most of the internal tuberosity is damaged or missing as well. Accordingly, Figure 18A should be interpreted as proximal aspect, with anterior facing to the left, and Figure 18B should be interpreted as anterior aspect (see Fig. 14B for comparison). Characters 305 and 306 in Appendix S2 should be re-coded from '0' to '?' for *Cryolophosaurus*. These corrections do not change the results or interpretations of the phylogenetic analysis reported here.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1. List of characters and character-states used in phylogenetic analysis.
Appendix S2. Taxon-character state data matrix used in the phylogenetic analysis.

This material is available as part of the online article from:
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