

Dinosaur remains from the La Quinta Formation (Lower or Middle Jurassic) of the Venezuelan Andes

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with 6 figures and 1 table

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Abstract: Dinosaur remains are exceptionally scarce in northern South America and Jurassic faunas from this area are particularly poorly known. We provide descriptions of new dinosaur specimens from a bonebed in the La Quinta Formation (Early or Middle Jurassic) of western Venezuela. The specimens are disarticulated and associations of elements are rare, but at least two distinct taxa appear to be present. Ornithischian dinosaurs are identified on the basis of isolated teeth and a distal tibia. The teeth represent a non-cerapodan basal ornithischian and possess a unique combination of character states, suggesting that they pertain to a new and unnamed taxon. Other remains represent an indeterminate basal saurischian (based on an ilium) and indeterminate dinosaurs (caudal vertebrae and a femur). The apparently plesiomorphic morphology of many of the dinosaurian remains is consistent with suggestions of an Early or Middle Jurassic age for the La Quinta Formation. Previous reports of the basal ornithischian *Lesothosaurus* sp. from the La Quinta Formation cannot be substantiated on the basis of available data.

Keywords: Dinosauria • Venezuela • Jurassic • La Quinta Formation

Kurzfassung: Dinosauria, vor allem Reste aus dem Jura, sind besonders selten im nördlichen Teil Südamerikas. Hier werden neue Dinosaurierreste aus einem Bonebed der La Quinta-Formation (Unter- oder Mitteljura) aus dem westlichen Venezuela beschrieben. Die Funde sind disartikuliert, und es gibt nur wenige assoziierte Elemente. Allerdings lassen sich die Reste mindestens zwei Taxa zuordnen. Ornithischia wurden anhand von isolierten Zähnen und dem distalen Teil einer Tibia identifiziert. Die Zähne gehören zu einem nicht-cerapoden, basalen Ornithischier, und sie besitzen eine einzigartige Kombination von Merkmalen, die wahrscheinlich diagnostisch für ein neues, unbeschriebenes Taxon sind. Andere Reste belegen einen basalen Saurischia indet. (Ilium) und Dinosauria indet. (Caudalwirbel und Femur). Die plesiomorphe Morphologie vieler der Dinosaurierreste stimmt mit vorgeschlagenen Altersschätzungen auf Unter- oder Mitteljura für die La Quinta-Formation überein. Bisherige Berichte über das Vorhandensein des basalen Ornithischiers *Lesothosaurus* sp. aus der La Quinta-Formation konnten anhand des untersuchten Materials nicht bestätigt werden.

Schlüsselwörter: Dinosauria • Venezuela • Jura • La Quinta-Formation

Introduction

Early and Middle Jurassic terrestrial vertebrate faunas are poorly known due to the rarity of suitable localities worldwide. Important Early Jurassic dinosaur faunas

are known from southern Africa (KITCHING & RAATH 1984), India (e.g. BANDYOPADHYAY & ROYCHOWDHURY 1996), the USA (TYKOSKI 2005) and China (YOUNG 1951; DONG 1992), while Middle Jurassic faunas have been recovered principally from the UK (PHIL-

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LIPS 1871; BENTON & SPENCER 1995), northern France (ALLAIN & PEREDA-SUPERBIOLA 2003), China (DONG et al. 1983; DONG 1992; CLARK et al. 2006) and Patagonia (BONAPARTE 1979; RAUHUT 2005). A number of other less productive sites of both ages are also known (summarised in WEISHAMPEL et al. 2004). Middle Jurassic localities have yielded remains of microvertebrates (including lissamphibians, rhynchocephalians, squamates, non-mammalian synapsids and mammals), crocodylians, turtles and pterosaurs (e.g. EVANS & MILNER 1994; EVANS & WALDMAN 1996; RAUHUT et al. 2002; CLARK et al. 2004, 2006; EVANS et al. 2006; MARTIN et al. 2006); rhynchocephalians, rare turtles, cynodonts, mammals, primitive crocodylians and pterosaurs are also known from the Early Jurassic (e.g. KITCHING & RAATH 1984; WELLNHOFER 1991; LUO & WU 1994; BANDYOPADHYAY & ROYCHOWDHURY 1996; EVANS et al. 2001; TYKOSKI 2005). Although some of these individual localities have a high species richness and may produce many individual specimens (e.g. EVANS & MILNER 1994; CLARK et al. 2006), the small number of productive localities and their limited geographical distribution severely restricts our view of vertebrate evolution during these intervals. This is unfortunate, as the available fossil record indicates that the Early and Middle Jurassic witnessed the first appearances or major radiations of clades that went on to become important components of late Mesozoic and, in some cases, Tertiary ecosystems. These groups include lissamphibians (EVANS et al. 1988, 1990), squamates (EVANS 1998, 2003), pterosaurs (KELLNER 2003), docodont mammals (e.g. KERMACK et al. 1987) and dinosaur clades, including ceratosaurian and tetanuran theropods (RAUHUT 2003; HOLTZ et al. 2004), eusauropod and neosauropod sauropods (WILSON 2002; UPCHURCH et al. 2004) and cerapodan ornithischians (BUTLER 2005). This conclusion is reinforced by phylogenetic analyses, which posit a large number of ghost lineages for these clades that extend through the Early to Middle Jurassic interval (see references listed above). In addition, several clades more characteristic of early Mesozoic ecosystems (including most non-mammalian synapsids and 'prosauropod' dinosaurs) became extinct or severely reduced in diversity at this time (e.g. OLSEN & SUES 1986). Consequently, discoveries of new localities yielding well-preserved terrestrial vertebrate material from these periods are particularly noteworthy as they have the potential to illuminate major evolutionary patterns.

The dinosaur fossil record of northern South America is exceptionally poorly known, especially in comparison with the rich faunas obtained from Argentina and southern Brazil (WEISHAMPEL et al. 2004). With the exception of rare associated and articulated theropod specimens from the Lower Cretaceous Santana Formation of Brazil (KELLNER & CAMPOS 1996; SUES et al. 2002; NAISH et al. 2004), known dinosaur material from northern South America consists of trackways and footprints (e.g. LEONARDI 1989; BUFFETAUT 2000) or

poorly-preserved, fragmentary skeletal material (e.g. LANGSTON & DURHAM 1955; MAWSON & WOODWARD 1907).

The La Quinta Formation of the Venezuelan Andes yields a dinosaur fauna that is of Early or Middle Jurassic age (SCHUBERT 1986; RUSSELL et al. 1992; SÁNCHEZ-VILLAGRA & CLARK 1994; MOODY 1997). As a consequence of its age and geographical location it has the potential to provide an important window on dinosaur evolution and palaeobiogeography. Previous authors have reported fragmentary ornithischian material (RUSSELL et al. 1992; SÁNCHEZ-VILLAGRA & CLARK 1994) and isolated indeterminate theropod teeth (MOODY 1997) from this unit. Here, we provide a preliminary report on a large sample of additional dinosaur specimens from the La Quinta Formation. This collection was mentioned briefly by SÁNCHEZ-VILLAGRA & CLARK (1994), and at least some of the remains were attributed to a small ornithischian dinosaur. Subsequent work, however, suggests that more than one dinosaur taxon is represented in the sample.

Abbreviations used in the text: BMNH, The Natural History Museum, London; MBLUZ, Museo de Biología de la Universidad del Zulia, Maracaibo; SAM, South African Museum, Iziko Museums of Cape Town, Cape Town.

Geological setting

The most comprehensive reviews of the La Quinta Formation have been provided by C. SCHUBERT and colleagues (SCHUBERT et al. 1979; SCHUBERT 1986) and the following summary is drawn from the work of these authors and the references cited therein. This unit lies unconformably on a middle Carboniferous to Permian sequence of metamorphosed sediments (Mucuchachí Formation) and is separated from overlying Cretaceous sediments (Rio Negro, Apón and Aguardiente formations) by a second unconformity. The type section of the La Quinta Formation, situated near the town of La Grita, western Venezuela, represents a series of continental, volcanic and localised marine/brackish sediments that were deposited in a series of restricted basins that formed during the initial stages of Pangaeon rifting in the early Mesozoic.

The type section reaches an estimated thickness of 1610 m, though in other areas thicknesses of up to 3400 m have been reported. At the type locality, the formation can be divided into three intervals: a basal tuff (150 m); an interval composed of interbedded sandstones, siltstones, tuffs and occasional limestones (840 m); and an upper section of sandstones and siltstones (620 m). Plant, palynomorph, ostracod and fish remains have been reported from the middle interval (SCHUBERT 1986). The different facies of the La Quinta Formation represent a series of distinct palaeoenvironments: for example, limestones were deposited under freshwater/brackish conditions and siltstones appear to

have been deposited on alluvial plains. Swampy, fresh-water lagoonal and semi-arid facies have also been identified.

The age of the La Quinta Formation has been difficult to establish due to the presence of several conflicting lines of evidence (SCHUBERT 1986). Radiometric dates based on the basal tuff layer show wide discrepancies: ^{40}K - ^{40}Ar dating provided age estimates of 122.5 ± 7.7 Ma (Aptian: Early Cretaceous) and 149.0 ± 10.0 Ma (Tithonian: Late Jurassic), while ^{207}U - ^{206}U methods provide a date of 229.0 ± 15.0 Ma (Ladinian: Middle Triassic). This wide range of dates suggests significant diagenetic alteration of the tuffs, though re-sampling and analysis with more sophisticated techniques may provide useful new results. Palynomorphs (*Classopollis papillatus*, *Circulina meyeriana* and *Caytopollis pallidus*) have been proposed to support a Late Triassic (Norian) to Late Jurassic age. Finally, plant macrofossils (*Dictyophyllum*, *Dictyozamites*, *Nilssonia*, *Ptilophyllum* and *Otozamites*) indicate an Early to Middle Jurassic age. Referral of dinosaur material from the formation to the genus *Lesothosaurus*, a taxon otherwise known from the Early Jurassic of southern Africa (SERENO 1991), was used to provide additional support for an Early Jurassic age (RUSSELL et al. 1992).

The materials reported herein come from the same bonebed as that reported by RUSSELL et al. (1992), which yielded the first reported dinosaur material from the La Quinta Formation. This bonebed is located in a small road cut across the Río La Grita from the type section of the formation, which, as described by SCHUBERT (1986), lies along the road between La Grita and Seboruca, in Táchira State. RUSSELL et al. (1992) mentioned that the bonebed is separated from the type section by a fault. MOODY (1997: 38) suggested that a second fault, roughly parallel to the Río La Grita and perpendicular to the strike of the first, may have further separated the bonebed from the type section. The section with the bonebed may correspond to the upper interval of the type section as described by SCHUBERT (1986), based on overall lithology, the presence of the same sedimentary structures and the lack of volcanic strata (see also MOODY 1997: 38). This contrasts with the interpretation of RUSSELL et al. (1992) who suggested that the bonebed was positioned in the middle interval of the formation. The material reported herein was collected by teams led by MRSV (1992, 1993) and JMM (1994). It occurs in a single bonebed composed of siltstone: when weathered this siltstone is green, but prepared and freshly broken blocks are purplish in colour.

Red siltstones containing numerous ganoid fish scales and disarticulated fish bones are found next to the bonebed. In this context, it is worth mentioning that KÜNDIG (1938) reported shark coprolites from the type section of the La Quinta Formation, which contain scales, plates, teeth, and palatine bones referable to *Lepidotes* (A.S. Woodward cited in KÜNDIG 1938; A.S.

Woodward, unpublished notes in the archives of the Palaeontology Department, Natural History Museum, London).

Description and comparisons

Although many individual elements are preserved in the collections from the La Quinta Formation, only a small number of these can be positively referred to Dinosauria on the basis of either comparative anatomy or the recognition of specific synapomorphies. Moreover, the lack of articulated specimens and the mixture of material from different individuals in single blocks (as indicated by the assortment of differently sized elements and the combined presence of elements from distinct taxa: Fig. 1) prevent the identification of unambiguous associations. We adopt a conservative approach herein and describe in detail only those specimens that can be referred to Dinosauria with reasonable confidence.

It is possible that some of the other elements in the collection also pertain to dinosaur or dinosauriform taxa, but as these specimens only possess characters with an equivocal phylogenetic distribution we provisionally identify them as either Reptilia indet. or Archosauria indet. (Tab. 1). For example, one isolated cervical vertebra (MBLUZ P1434: Fig. 1A) and several isolated dorsal vertebrae (MBLUZ P978, P1102, P1340, P1515: Fig. 2) possess well-defined centrodiaepophyseal, pre- and postzygapophyseal and spinopostzygapophyseal laminae, features that are present in saurischian dinosaurs (WILSON 1999). However, similar laminae are also present in other non-dinosaurian archosaurs, including *Arizonasaurus*, *Effigia* and *Silesaurus* (DZIK 2003; NESBITT 2005, 2007). Consequently, although the morphology of these vertebrae is consistent with a dinosaurian origin, we refrain from referring them to Saurischia on the basis of current data and refer them to Archosauria incertae sedis. It is hoped that future collections from the La Quinta Formation will provide the associations needed to allow such indeterminate material to be identified more fully.

Some of the elements described below occur in the same blocks (e.g. Fig. 1): consequently, several different elements bear the same collection number.

Postorbital: A left postorbital (MBLUZ P1504: Fig. 3) represents the only cranial bone in the collection that may be referred to Dinosauria. It is a triradiate element in lateral view, consisting of rostral, ventral and caudal processes. The rostral margin of the element forms the smoothly concave orbital margin; the dorsal border forms the lateral margin of the supratemporal fenestra; and the caudal margin represents the rostrorodorsal boundary of the infratemporal fenestra. Both the rostral and ventral processes are slender and elongate, tapering to a sub-triangular point in lateral view. In contrast, the caudal process terminates in a broadly rounded apex.

Tab. 1. Reptile material from the La Quinta Formation housed in the collections of the Museo de Biología de la Universidad del Zulia (MBLUZ), Maracaibo, Venezuela.

Specimen	Element(s) preserved	Identification
P958	Phalanx	Reptilia indet.
P962	Premaxillary tooth	Ornithischia indet.
P978	Dorsal vertebra	Archosauria indet.
P982	Ectopterygoid(?)	Reptilia indet.
P1062	Maxillary/dentary tooth	Ornithischia indet.
P1068	Sacral vertebral centrum	Reptilia indet.
P1069	Cervical vertebral centrum	Reptilia indet.
P1072	Maxillary/dentary tooth	Ornithischia indet.
P1085	Maxillary/dentary tooth	Ornithischia indet.
P1086	Scapula and indeterminate bone fragments	Reptilia indet.
P1089	Phalanx	Reptilia indet.
P1090	Osteoderm	Reptilia indet.
P1094	Maxillary/dentary teeth (two)	Ornithischia indet.
P1095	Distal right tibia	Ornithischia indet.
P1098	Maxillary/dentary tooth	Ornithischia indet.
P1100A	Distal caudal vertebra	Dinosauria indet.
P1101	Block with left scapula and coracoid and rib fragments	Reptilia indet.
P1102	Dorsal vertebra and indeterminate bone fragments	Archosauria indet.
P1104	Phalanx	Reptilia indet.
P1337	Premaxillary(?) tooth	Ornithischia indet.
P1339	Phalanx	Reptilia indet.
P1340	Distal caudal vertebra and a dorsal vertebra	Dinosauria indet. (caudal); Archosauria indet. (dorsal)
P1341	Anterior caudal vertebra	Dinosauria indet.
P1344	Caudal vertebral centrum	Reptilia indet.
P1350	Axis	Reptilia indet.
P1352	Caudal vertebra	Dinosauria indet.
P1353	Broken neural arch	Reptilia indet.
P1354	Caudal vertebral centrum	Reptilia indet.
P1395	Maxillary/dentary tooth	Ornithischia indet.
P1396	Maxillary/dentary tooth	Ornithischia indet.
P1397	Maxillary/dentary tooth	Ornithischia indet.
P1398	Maxillary/dentary tooth	Ornithischia indet.
P1400	Maxillary/dentary tooth	Ornithischia indet.
P1401	Premaxillary tooth	Ornithischia indet.
P1434	Block containing a distal femur, proximal tibia, fibula, cervical vertebral centrum, premaxillary tooth, maxillary/dentary tooth, ischium(?), chevron, ribs	Archosauria indet. (cervical); Ornithischia indet. (teeth); Reptilia indet. (remainder)
P1437	Right quadrate and indeterminate bone fragment	Reptilia indet.
P1443	Block containing a left ilium, caudal vertebral centrum, phalanx and indeterminate bone fragments	Saurischia indet. (ilium); Reptilia indet. (remainder)
P1473	Ungual phalanx	Reptilia indet.
P1490	Distal right femur	Reptilia indet.
P1503	Right quadrate and caudal vertebra	Reptilia indet.
P1504	Left postorbital	Dinosauria indet.
P1506	Ilium(?)	Reptilia indet.
P1507	Ungual phalanx	Reptilia indet.
P1515	Block containing a large metatarsal, ribs, a dorsal vertebra, caudal vertebrae, a chevron, and a sacral(?) neural arch	Archosauria indet. (dorsal); Dinosauria indet. (caudals); Reptilia indet. (remainder)
P1554	Phalanx	Reptilia indet.
P1555(1)	Ilium(?), premaxillary tooth, neural arch and rib fragments	Ornithischia indet. (tooth) Reptilia indet. (remainder)
P1555(2)	Two caudal vertebrae, a phalanx and ribs	Dinosauria indet. (caudals); Reptilia indet. (remainder)
Unnumbered	Fragmentary limb material (including a proximal femur), pelvic material, partial vertebrae, ribs, two maxillary/dentary teeth and a phalanx	Dinosauria indet. (femur); Ornithischia indet. (teeth); Reptilia indet. (remainder)

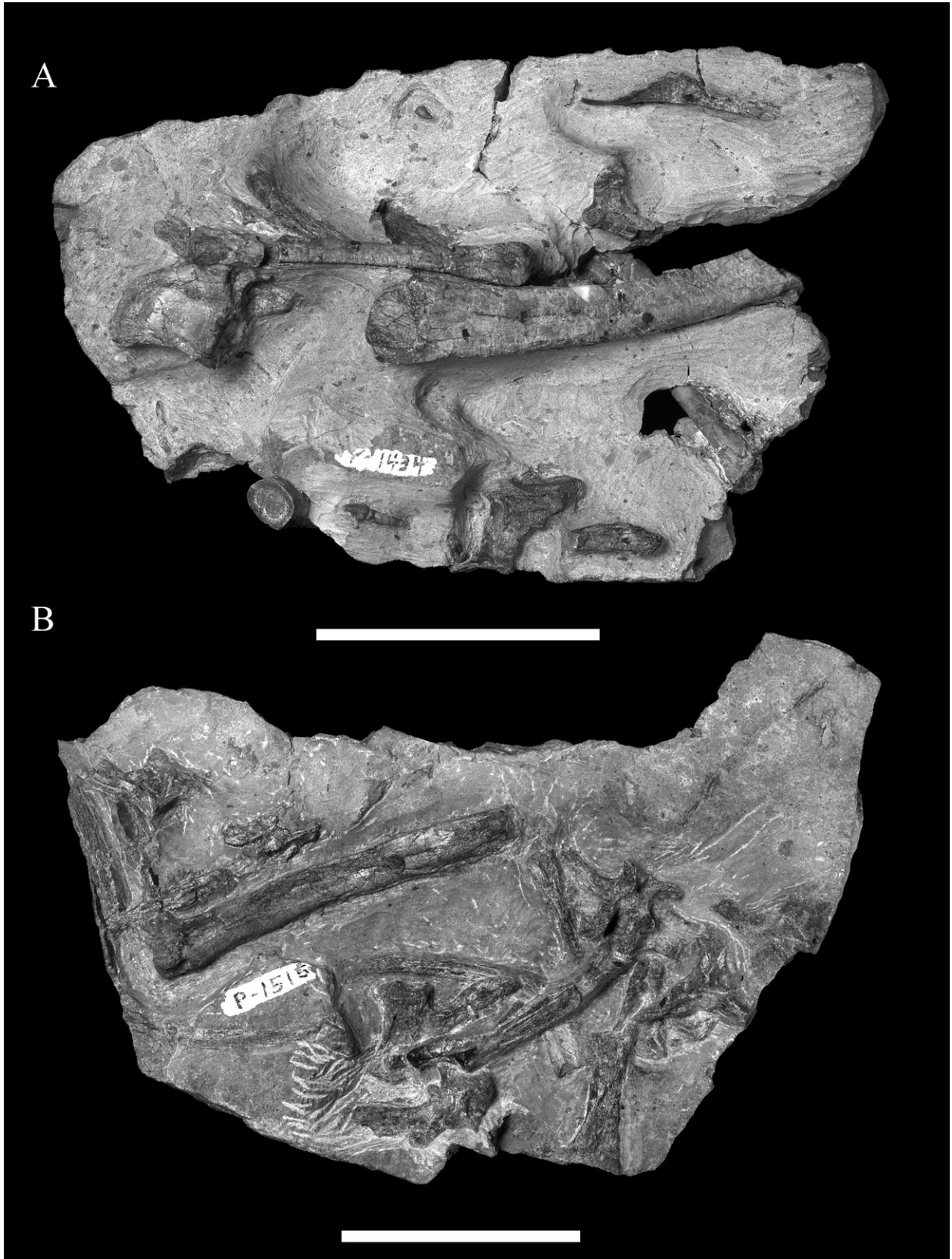


Fig. 1. Representative blocks of matrix collected from the La Quinta Formation bonebed containing disarticulated, largely unassociated collections of small reptile bones. **A:** MBLUZ P1434, containing a cervical vertebra from an indeterminate archosaur (positioned far left), an indeterminate ornithischian cheek tooth, and assorted indeterminate limb and girdle material. **B:** MBLUZ P1515, containing indeterminate dinosaur caudal vertebrae, an indeterminate archosaur dorsal vertebra (not visible in this orientation), and assorted indeterminate limb and axial elements. – Scale bars = 50 mm.

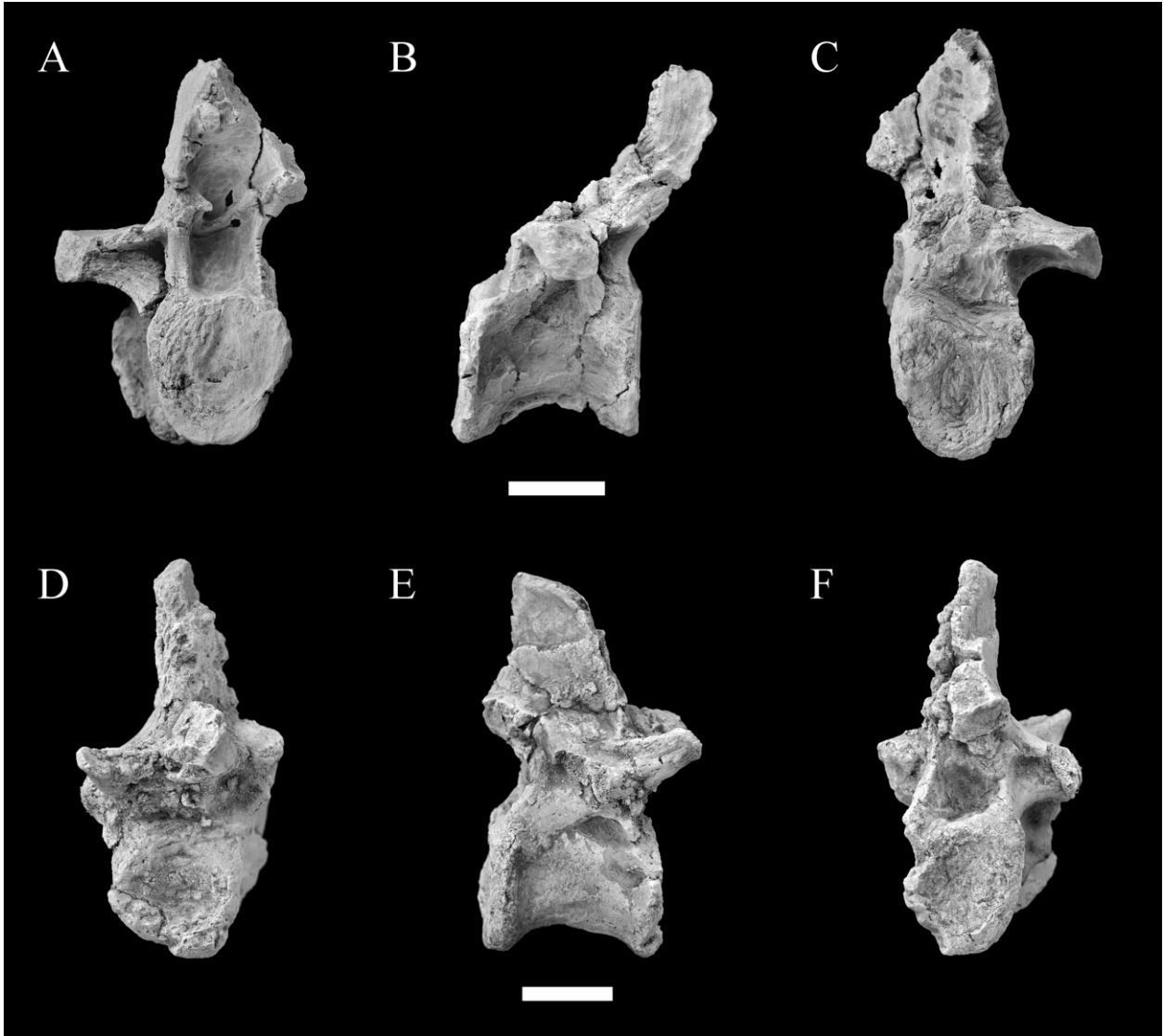


Fig. 2. Indeterminate archosaur dorsal vertebrae in anterior (A, D), right lateral (B, E) and posterior (C, F) views. **A–C:** MBLUZ P978. **D–F:** MBLUZ P1340. – Scale bars = 10 mm.

The ventral process is the longest, but it is only slightly longer than the rostral process: the short caudal process is approximately 50% of the length of the ventral process. In lateral view, angles of approximately 120, 100 and 140 degrees separate the ventral and rostral processes, rostral and caudal processes and caudal and ventral processes, respectively. The lateral surfaces of the ventral and rostral processes are planar to very gently convex, while that of the caudal process is strongly convex. In dorsal view, the caudal process curves medially. The postorbital bears no rugosities or tuberosities on its lateral surface. The medial, rostral and caudal borders of the element are obscured by matrix.

All dinosaurs lack a postfrontal bone (SERENO & NOVAS 1994). As a consequence the rostral process of the dinosaur postorbital is much more elongate than in other reptiles (e.g. ROMER 1956). The long slender rostral process of P1504 is consistent with referral to Dinosauria. In addition, the absence of a rugosity on the lat-

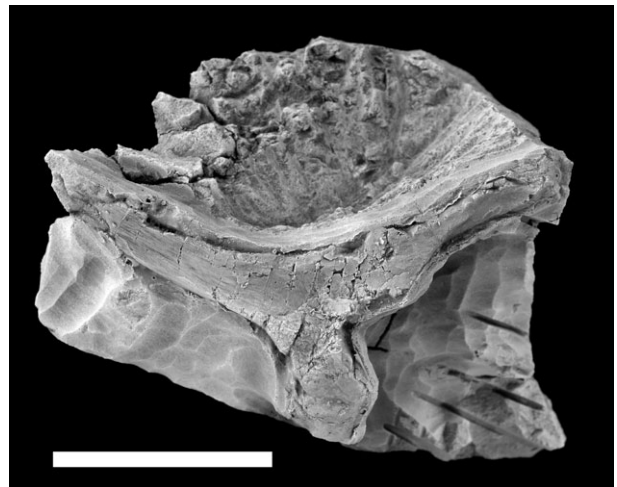


Fig. 3. A left postorbital (MBLUZ P1504) from an indeterminate dinosaur. Rostral is to the left. – Scale bar = 20 mm.

eral surface of the postorbital suggests that referral to Neotheropoda is unlikely: neotheropods generally possess a rugosity at the caudodorsal corner of the orbit, even if only weakly developed (O.W.M. RAUHUT, pers. comm.). No other features of the postorbital permit it to be assigned to any more exclusive clade and we regard this element as *Dinosauria incertae sedis*.

Dentition: Several probable premaxillary tooth crowns have been identified. MBLUZ P1401 lacks its root and apex, but the crown is gently recurved, with a convex mesial surface and a weakly concave distal surface. The labial crown surface is convex apicobasally whereas the lingual crown surface is apicobasally concave; as a result, the apex of the crown is directed slightly medially. The crown is gently expanded above the broken base of the root in both mesiodistal and apicobasal directions. Denticles are absent from mesial and distal surfaces. Weak apicobasally extending ridges and associated furrows are present on both labial and lingual surfaces, as in the cheek teeth (see below). P962, P1434 (one of two teeth exposed on this block) and P1555(1) are incompletely exposed but appear generally similar to P1401 and may also represent premaxillary teeth. P1337 may represent either a more distal premaxillary tooth or an anterior maxillary tooth: it is recurved and its apex is directed weakly medially, but it differs from P1401 in being more strongly transversely compressed and possessing a few weak denticles on mesial and distal margins.

Fourteen other teeth (MBLUZ P1062, 1072, 1085, 1094 [two teeth], 1098, 1395, 1396, 1397, 1398, 1400, P1434 [one of two teeth exposed on this block] and two unnumbered specimens) appear to be from either the dentary or maxillary tooth row (Fig. 4). As these teeth are isolated, it is not possible to identify whether they are from the maxilla or dentary or if they are from the right or left tooth row. Comparisons with the basal ornithischian *Lesothosaurus* (SERENO 1991) provides some basis for distinguishing between labial and lingual surfaces (see below). The maxillary/dentary teeth show a range of variation: however, this is limited to variation in the apicobasal height of the crowns and there is no evidence to contradict the hypothesis that all of these crowns belong to a single taxon. Consequently, we provide descriptions of two representative crowns (MBLUZ P1062, 1396), rather than describing each individual crown separately.

Only the crown of MBLUZ P1062 is preserved (Figs. 4A–D); the root is broken and missing. The apex of the crown is also missing, and examination of the broken surface demonstrates that the thin layer of enamel was distributed symmetrically on labial/lingual surfaces. As the apex is missing it is difficult to assess the presence or absence of recurvature (as present in at least some other crowns, see below) and to identify mesial/distal surfaces. As preserved, the apicobasal height of the crown slightly exceeds its mesiodistal width. The

crown base is swollen and expanded above the root both mesiodistally and labiolingually (forming a “cingulum”). This basal labiolingual swelling is asymmetrical in mesial/distal view and is more bulbous and set slightly further from the crown apex on one side (identified here as the labial surface, by comparison with *Lesothosaurus*: SERENO 1991).

Denticles are present along the mesial and distal surfaces of the crown, although they are only well-preserved on one side (they have broken away on the other). Five denticles are present on the better-preserved surface. The basalmost denticle is supported lingually and labially by weak marginal ridges that merge with the basal crown swelling. These marginal ridges form the margins of flat to concave “interdental pressure facets” that indicate the presence of imbricated adjacent teeth along at least part of the tooth row.

Around six apicobasally extending ridges are present on the lingual and labial surfaces of the crown. The ridges are low, sub-parallel, sub-equal in mesiodistal width, are separated from one another by shallow furrows and extend from the broken apex of the crown to the basal swelling. These ridges give the labial and lingual surfaces a corrugated appearance in cross-section. The enamel of the lingual and labial surfaces is additionally covered with fine wrinkles or striations.

The apex of MBLUZ P1396 is missing, but the crown is apicobasally tall (apicobasal height is approximately 133 % of mesiodistal width) and weakly recurved with the apex offset slightly posteriorly (Figs. 4E–H). Apicobasal crown height is greatest in the similar crown MBLUZ P1098, in which apicobasal height is at least 150% of mesiodistal width.

Based on the recurvature it is possible to identify mesial and distal surfaces; the mesial margin is slightly longer than the distal. The crown base is swollen and expanded above the root both mesiodistally and labiolingually. This basal labiolingual swelling is asymmetrical in mesial/distal view and is more bulbous and set slightly further from the crown apex on the labial side. The labial crown surface is strongly convex mesiodistally. Lingually, the central crown surface is also convex mesiodistally. However, the surface of the lingual crown is depressed and concave adjacent to the mesial and distal denticle rows. Six vertical apicobasally extending ridges are present on the labial crown surface. These ridges extend from the basal swelling to the apex, and converge apically. The ridges are low and rounded, and separated from one another by shallow vertical furrows. Apicobasally extending ridges are also present on the lingual crown surface, although they are much more weakly developed. As in many of the other crowns, the surface of the enamel is covered with numerous small apicobasally extending wrinkles.

Denticles are present along the mesial and distal crown margins. Six are present on the mesial margin, but appear to have been restricted to the basal 70% of the crown. Denticles are poorly preserved along the dis-

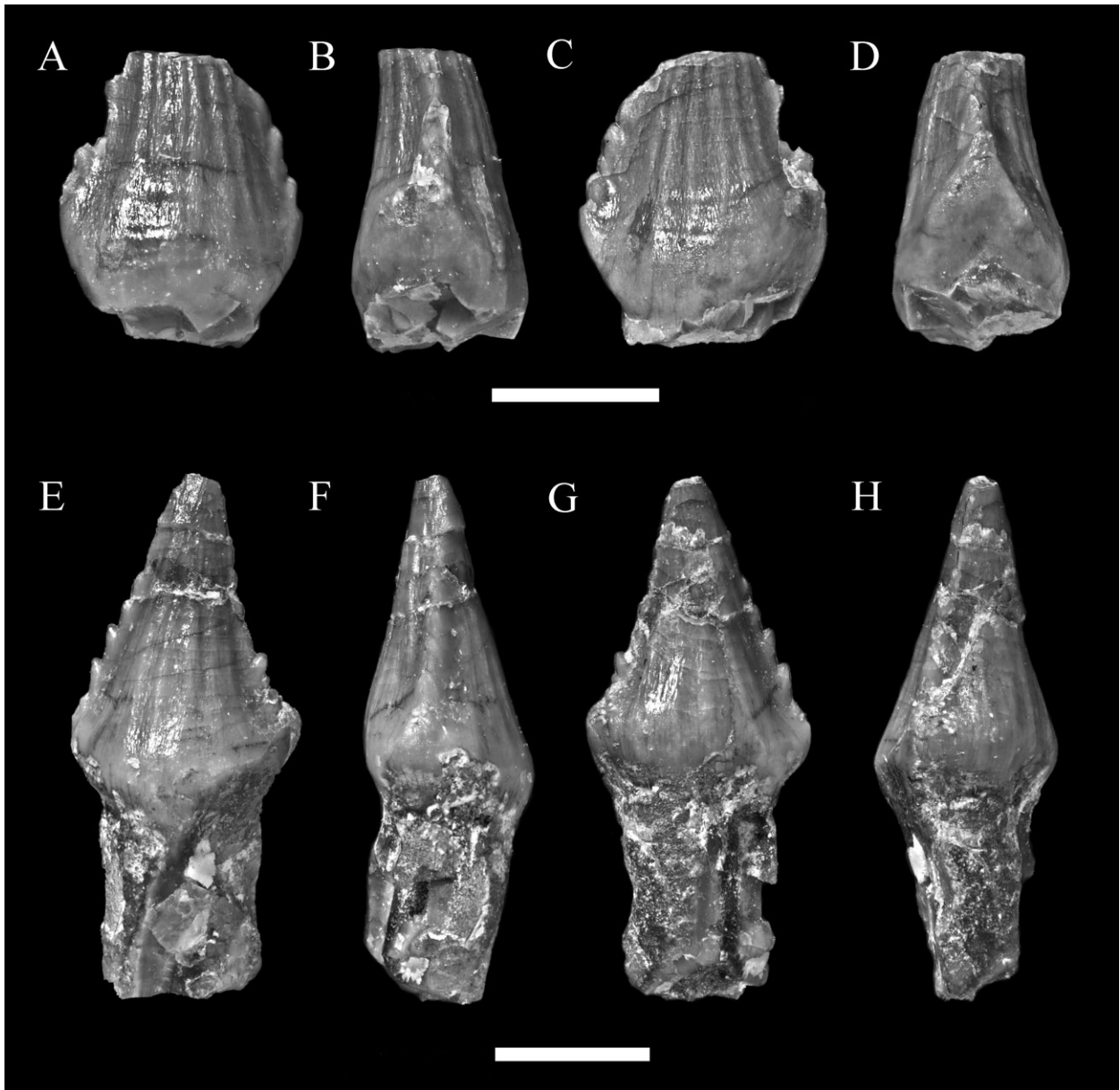


Fig. 4. Maxillary/dentary teeth of an indeterminate ornithischian dinosaur in labial (A, E), lingual (C, G), mesial/distal (uncertain as it is unknown whether these are maxillary or dentary teeth: B, D), mesial (F) and distal (H) views. – A–D: MBLUZ P1062. E–H: MBLUZ P1396. – Scale bars = 2 mm.

tal margin, but also appear to have been restricted to the basal 70 % of the crown. The most basal denticles are supported lingually by subtle marginal ridges confluent with the basal swelling. ‘Interdental pressure facets’ are not well-developed, unlike the condition in MBLUZ P1062 (see above).

Both the premaxillary and cheek teeth strongly resemble those of basal ornithischians (e.g. SERENO 1991). They possess a large number of features often considered synapomorphic for Ornithischia (e.g. SERENO 1986, 1991; HUNT & LUCAS 1994; HECKERT 2002, 2004; NORMAN et al. 2004), including: low maxillary/dentary crowns that have sub-triangular outlines in labial view (present in at least some crowns); maxillary/

dentary crowns expanded labiolingually above the roots to form a ‘cingulum’ supported mesially and distally by ridges; maxillary/dentary crowns expanded mesiodistally above roots such that the maximum mesiodistal length of the crown is greater than the maximum mesiodistal length of the root (presence of a “neck”); maxillary/dentary crowns asymmetrical in mesial and distal views; maxillary/dentary crowns with enlarged denticles on the mesial and distal margins; maxillary and dentary crowns with an associated “interdental pressure facet” suggesting an en echelon arrangement in the jaw. Although some of these features occur in non-dinosaurian Triassic archosaurs (DZIK 2003; PARKER et al. 2005; BUTLER et al. 2006; IRMIS et al. 2007), the major-

ity of these features have not yet been documented in non-ornithischian Jurassic archosaurs. Additionally, recent reviews have considered the presence of a “cingulum” supported mesially and distally by ridges that connect to the basal-most denticles as a valid ornithischian synapomorphy (BUTLER et al. 2006; IRMIS et al. 2007). As this latter feature is present in the teeth from the La Quinta Formation, we identify these specimens as ornithischian dinosaurs.

The La Quinta teeth can be distinguished from those of other ornithischians. They differ from those of the basal ornithischian *Lesothosaurus* (SERENO 1991), basal thyreophorans (*Scutellosaurus*, COLBERT 1981; *Emausaurus*, HAUBOLD 1990; *Scelidosaurus*, BARRETT 2001), and the basal neornithischian *Agilisaurus* (BARRETT et al. 2005), in possessing apicobasally extending ridges on labial and lingual surfaces. Additionally, at least some of the crowns have apicobasal heights that significantly exceed mesiodistal widths; in contrast, *Lesothosaurus* and basal thyreophorans have tooth crowns with apicobasal heights that are approximately equal to their mesiodistal widths. Apicobasally tall crowns and apicobasally extending ridges are present in the Chinese Middle Jurassic ornithischian *Hexinlusaurus* (HE & CAI 1984; BARRETT et al. 2005) and the Late Triassic basal dinosauriform *Silesaurus* (DZIK 2003). However, in *Hexinlusaurus* the crowns are chisel-shaped with denticles that are restricted to the apical half of the crown and in *Silesaurus* the teeth lack asymmetrical cingula. The teeth of most cerapodan ornithischians differ from the La Quinta teeth in their possession of asymmetrically distributed enamel (SERENO 1986). The unique combination of characters present in the La Quinta teeth suggests that they represent a taxon distinct from known ornithischian dinosaurs. However, given the fragmentary nature of the available material and the uncertainty as to whether or not all of the teeth pertain to a single species, we refrain from providing a name or formal diagnosis for this taxon.

Caudal vertebrae: Many caudal vertebrae are present in the collection, representing elements from the proximal, middle and distal parts of the tail. Most of the caudal vertebrae appear to be from the same taxon as many exhibit elongation of the neural spine (see below), though this conclusion should be regarded as preliminary given the lack of associations between elements. Several isolated caudal centra and neural arches (MBLUZ P1344, 1354, 1443, 1515 [in part] and 1555[2]) cannot be referred to this taxon on the basis of the available material and are provisionally referred to *Reptilia incertae sedis*. However, other caudal vertebrae are likely to pertain to dinosaurs (MBLUZ P1100A, 1340, 1341, 1352, 1515 [in part] and 1555[2]). It should be noted that many of these vertebrae occur in blocks containing a mixture of elements.

The centra are amphicoelous to amphiplatyan with shallowly excavated lateral surfaces (Fig. 5). The centra

are not strongly constricted and bear a broad, rounded midline keel (where visible: the ventral surfaces of many caudals are obscured by matrix). More proximally positioned caudals (e.g. MBLUZ P1341) have centra that are relatively short relative to their width and sub-circular to shield-shaped anterior and posterior articular surfaces that are approximately as wide as they are high. Middle and distal caudals (e.g. MBLUZ P1340 and MBLUZ P1555[2]) have more elongate centra that are more than twice as long as they are wide. In addition, middle and distal caudal centra are mediolaterally compressed with consequent narrowing of the articular surfaces. In these centra, the articular surfaces have an elongate sub-elliptical or sub-rectangular outline and are taller than they are wide. Neurocentral sutures are visible in some of the vertebrae. Small crescentic or trapezoidal chevron facets are present ventral to the intervertebral articulations on the anterior and posterior surfaces of proximal and middle caudals, but are absent from the best-preserved distal caudal (MBLUZ P1340).

The neural arches of all caudals are relatively simple in structure and lack vertebral laminae. Prezygapophyses are elongate and extend anterodorsally from the neural arch at an angle of approximately 45 degrees to the horizontal. In proximal caudals, the prezygapophyses diverge from each other in anterior view, whereas in more distal caudals they are closely appressed and extend parallel to each other. The postzygapophyses are

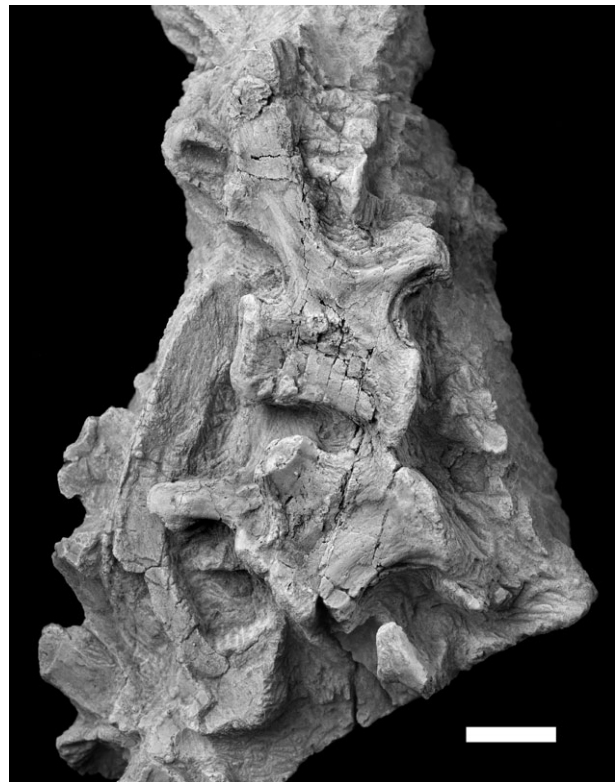


Fig. 5. Caudal vertebrae of an indeterminate dinosaur in lateral view (MBLUZ P1555[2]). Note the presence of other indeterminate elements in the same block. – Scale bar = 10 mm.

positioned dorsal to the level of the prezygapophyses. They do not form distinct processes, but are merely small articular facets situated approximately halfway along the posterior margin of the dorsoventrally expanded neural spine. Distal caudals lack clear postzygapophyseal facets. In all caudals, the neural spine is mediolaterally flattened, parallel sided in lateral view, and terminates in a bluntly rounded, unexpanded apex (Fig. 5). It projects posterodorsally at an angle varying from approximately 30 to 60 degrees depending on the position in the caudal series (neural spines of proximal and middle caudals are inclined more steeply than those of the distal caudals). As a result of neural spine elongation, the height of the neural arch as a whole is greater than that of the centrum in proximal and middle caudals. In some middle caudals, the total height of the neural spine is equal to three times that of the centrum, though in distal caudals neural arch height is approximately equal to that of the centrum. Proximal and middle caudals bear an anteroposteriorly short, sheet-like transverse process, with a narrow sub-elliptical cross-section. In middle caudals, this structure is reduced to a small bony process on the side of the neural arch and it is absent in distal caudals.

The middle and proximal caudal vertebrae (MBLUZ P1341, 1515 and 1555[2]) bear a striking resemblance to those of the basal ornithischian *Stormbergia* (BUTLER 2005; BMNH R11000), the basal ornithopod *Hypsilophodon* (GALTON 1974; BMNH R196) and the basal sauropodomorph *Thecodontosaurus* (BENTON et al. 2000). Corresponding caudal vertebrae of small theropods generally lack such elongate neural spines and have anteroposteriorly broad transverse processes (e.g. OSTROM 1978; COLBERT 1989). The dorsal positioning of the pre- and postzygapophyses on the neural arch of MBLUZ P1341, 1515 and 1555[2] differs from the situation in the middle caudal vertebrae of *Silesaurus* (DZIK 2003): in the latter, the pre- and postzygapophyses are situated more ventrally. Although distinct autapomorphies cannot be identified, the general phenetic resemblance of these caudals to those of *Hypsilophodon*, *Stormbergia* and *Thecodontosaurus* prompts us to refer these specimens to Dinosauria incertae sedis. The marked elongation of the neural spine in the distal caudal vertebrae (MBLUZ P1100A, 1340 and 1352) suggests that they may also be referable to the same taxon.

Ilium: A left ilium is preserved on a block containing various different elements, including a phalanx and caudal centrum (MBLUZ P1443: Figs. 6A, F). The ilium lacks the lateral portions of the ischiadic peduncle and the distal extremities of the anterior and posterior iliac processes. Although incomplete, the dorsal and ventral margins of the anterior iliac process appear to converge slightly, suggesting that the ilium was either brachyiliac (our preferred interpretation) or very weakly dolichoiliac. In either case, it is clear that the anterior iliac process was not dorsoventrally expanded relative to the

main body of the ilium. The main body of the ilium is relatively deep and sub-equal in height to the length of the pubic peduncle. In lateral view, the dorsal margin of the ilium is gently convex along its entire length. A supracetabular crest is present, but very poorly developed; as a result it does not strongly overhang the dorsal margin of the acetabulum. An angle of approximately 80 degrees separates the ventral margin of the anterior iliac process and the anterior margin of the pubic peduncle.

The pubic peduncle is slender and elongate. It extends ventrally and slightly anteriorly and has a sub-triangular cross-section. The distal end of the peduncle is slightly expanded anteroposteriorly relative to the shaft of the process. An extensive sheet of bone backs the acetabulum medially. This structure is broken ventrally so its exact limits cannot be determined, but it seems likely that the ventralmost part of the acetabulum was open. Posterior to the acetabulum, a well-developed horizontal brevis shelf is present on the lateral surface of the ilium, which forms the lateral margin of a deep brevis fossa. The medial margin of the brevis fossa is provided by the medial margin of the posterior iliac process, which extends further ventrally than the corresponding lateral margin of the latter. In ventral view, the lateral and medial margins of the brevis fossa diverge slightly as they extend posteriorly.

The presence of a brevis shelf and a partially open acetabulum are both considered dinosaur synapomorphies (e.g. BENTON 2004). However, in the majority of dinosaurs the acetabulum is fully open: the partially closed condition is found only among primitive saurischians (LANGER 2003, 2004) and basal ornithischians (BUTLER 2005). Nevertheless, several features of MBLUZ P1443 indicate that it cannot be referred to Ornithischia. Firstly, all ornithischians possess a dorsoventrally shallow, strap-like anterior iliac process (e.g. SERENO 1986). Although this area is broken in MBLUZ P1443, the remaining portion of the process is considerably deeper than would be expected in an ornithischian. Secondly, in lateral view, the dorsal margins of basal ornithischian ilia are typically straight (e.g. BUTLER 2005), whereas the dorsal margin of MBLUZ P1443 is convex. Finally, in basal ornithischians such as *Stormbergia* (BMNH R11000), *Scelidosaurus* (BMNH R1111), *Heterodontosaurus* (SAM-PK-K1332) and *Lesothosaurus* (BMNH RUB17), the pubic peduncles extend more strongly anteriorly than that of MBLUZ P1443.

Derived sauropods and tetanuran theropods possess dorsoventrally expanded anterior iliac blades and an open acetabulum (e.g. RAUHUT 2003; HOLTZ et al. 2004; UPCHURCH et al. 2004), so referral to either of these groups is not tenable. However, the character combination present in MBLUZ P1443 is consistent with referral to either a basal dinosaur or a basal saurischian, although it should be noted that the only proposed saurischian iliac synapomorphy (presence of a well developed supracetabular crest: LANGER 2004) is absent from the material. Several early saurischians, including the basal taxa

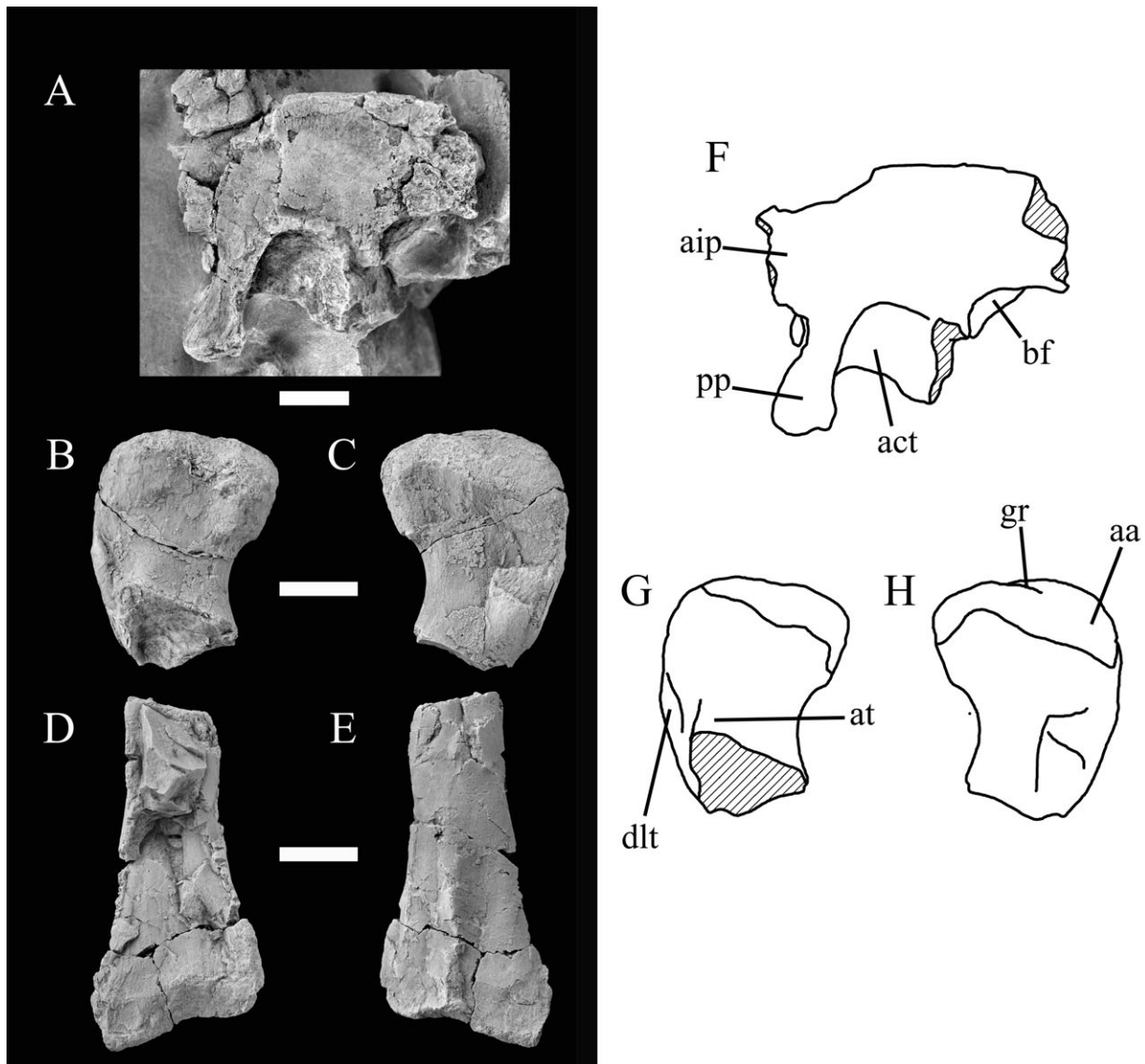


Fig. 6. Limb and pelvic girdle elements of small dinosaurs from the La Quinta Formation. **A:** Left ilium of an indeterminate saurischian dinosaur (MBLUZ P1443 [in part]) in lateral view. **B–C:** Proximal portion of a right femur (MBLUZ unnumbered: Dinosauria indet.) in anterior (B) and posterior (C) views. **D–E:** Distal end of a right tibia (MBLUZ P1095L *Ornithischia* indet.) in anterior (D) and posterior (E) views. **F:** Interpretative line drawing of left ilium (MBLUZ P1443 [in part]). **G–H:** Interpretative line drawings of the proximal right femur in anterior (G) and posterior (H) views. – Abbreviations: aa, articularis antitrochanterica; act, acetabulum; aip, anterior iliac process; at, anterior trochanter; bf, brevis fossa; dlt, “dorsolateral” trochanter; gr, groove on proximal surface of femur; pp, pubic peduncle. – Scale bars = 10 mm.

Herrerasaurus, *Staurikosaurus*, *Guaibasaurus* and *Chindesaurus* and the basal sauropodomorph *Saturnalia*, possess brachyliac ilia with a partially closed acetabulum (LANGER 2003, 2004). It appears likely that the ilium MBLUZ P1443 is referable to a primitive saurischian, but the absence of additional anatomical information prevents a more detailed identification.

Femur: The collection contains the proximal part of a small right femur (MBLUZ unnumbered: Figs. 6B–C, G–H). The proximal end of the element is expanded transversely and compressed anteroposteriorly. In proximal view, the anteroposterior width of the proximal end

is greatest laterally and tapers medially. The posterior surface is flat to weakly convex; the anterior surface is strongly convex. A low groove extends transversely across the proximal surface of the femur and separates the head into a posteromedial area and a strongly convex anterolateral area. LANGER (2003) documented this groove in a range of basal dinosaurs and suggested that the posteromedial area of the head articulated with the body of the ilium, and the anterolateral area of the head articulated with the supracetabular buttress. This groove is continuous with a depression on the posterolateral corner of the proximal femur that represents the articular surface for the iliac antitrochanter (fossa trochanter-

ica of NOVAS [1996]; articularis antitrochanterica of LANGER [2003]). Medially there is a broad and shallow sulcus for the ligamentum capitis femoris.

A low, proximodistally extending, crescent-shaped ridge is present on the anterolateral surface of the femoral head, as in all other basal dinosaurs (SERENO 1991; NOVAS 1993; LANGER 2003) and referred to as the “dorsolateral trochanter” by LANGER (2003) and LANGER & BENTON (2006). In ornithischians, the dorsolateral trochanter is drawn-out anteriorly into a distinct flange (e.g. SERENO 1991). Anteromedial and distal to the dorsolateral trochanter there is a low bulge on the anterior surface of the femur that represents part of the anterior trochanter. Unfortunately, the femur is broken through the anterior trochanter so it is not known if the ‘trochanteric shelf’ seen in basal dinosauriformes and basal saurischians was present or absent, or to determine the degree of development of the anterior trochanter. An additional low bulge is present on the posterolateral margin of the shaft, but the relationship of this structure to the trochanteric shelf is uncertain.

The absence of a well-defined medial tuberosity on the posterior aspect of the head and the inturned femoral head support the dinosaurian affinities of this femur (NOVAS 1996). Most of the other features preserved are plesiomorphic among dinosaurs. The proximal groove, articularis antitrochanterica, dorsolateral trochanter and anterior trochanter are all present in basal saurischians (NOVAS 1993), basal theropods (RAUHUT 2003), basal sauropodomorphs (LANGER 2003), and basal ornithischians (SERENO 1991). The weak anterior development of the dorsolateral trochanter and the medial position of the anterior trochanter indicate that this specimen does not pertain to Ornithischia. Unlike the condition in all neotheropods (RAUHUT 2003), the sulcus for the ligamentum capitis femoris is shallow and is not bound medially by a well-developed posterior lip. EZCURRA (2006) used the absence of a deep sulcus for the ligamentum capitis femoris as a basis for excluding the problematic dinosauriform *Eucoelophysius baldwini* from Neotheropoda. Although the morphology of the femur is not inconsistent with the morphology of basal saurischians (e.g. NOVAS 1993) and basal sauropodomorphs (LANGER 2003), we are unable to identify any synapomorphic characters that might link it with a specific dinosaurian clade. As a result, we consider the femur as Dinosauria indet.

Tibia: MBLUZ P1095 represents the distal end of a right tibia that has suffered *post mortem* anteroposterior compression (Figs. 6D–E). The distal end of the tibia is strongly expanded transversely relative to the shaft, and is triangular in distal view, with a relatively flat anterior surface, and a convex posterior surface, the apex of which extends proximally along the posterior margin of the shaft as a sharp and well-defined ridge. Proximally this ridge shifts medially and would probably have merged with the inner condyle of the proximal end (as occurs in *Stormbergia*, SAM-PK-K1105).

The lateral malleolus extends further distally and is broader transversely and narrower anteroposteriorly than the medial malleolus. A broad bevelled surface extends across the anteroventral surface of the medial malleolus and on to the anteromedial surface of the lateral malleolus; this surface represents the articular surface for the astragalus. Proximally, this surface is bounded by a low horizontal ridge that extends transversely across the medial malleolus. The nearly horizontal inclination of this low ridge indicates that the ascending process of the astragalus was low and weakly developed. The flat anterior surface of the distal tibia is interrupted by a distinct raised eminence, positioned at the lateral edge of the medial malleolus. Comparison with basal ornithischians (*Lesothosaurus* [BMNH RUB17]; *Eocursor* [SAM-PK-K8025; BUTLER et al. 2007]) suggests that this low eminence articulated with the weakly developed ascending process of the astragalus and the distal end of the fibula.

The strong transverse expansion of the distal end of MBLUZ P1095 is seen in ornithischians and a variety of theropods (RAUHUT 2003; LANGER & BENTON 2006). As in ornithischians, the ridge proximally delimiting the articular facet for the astragalus is horizontal, and the corresponding ascending process of the astragalus would have been low and poorly developed. This contrasts with the general theropod condition in which the corresponding ridge extends proximolaterally from the mediolateral corner of the tibia across the anterior surface of the shaft and there is a corresponding well-developed ascending process of the astragalus (e.g. RAUHUT 2003: figs. 44C, 49). In addition, the raised eminence at the anterolateral edge of the medial malleolus is present in basal ornithischians, but not in theropods. In light of these similarities, we identify MBLUZ P1095 as an indeterminate ornithischian dinosaur.

Discussion and conclusions

New material from the La Quinta Formation confirms the presence of at least two dinosaur taxa in the assemblage: a primitive non-cerapodan ornithischian (based on maxillary/dentary teeth) and an indeterminate saurischian (based on ilium). Other ornithischian (tibia) and dinosaur (vertebrae, femur) material in this collection and previously described specimens (RUSSELL et al. 1992; MOODY 1997) may be referable to these taxa or might represent additional diversity. Collection of unambiguously associated material is needed to test each of these possibilities. Although the ornithischian teeth described herein are distinctive and can be distinguished from those of other taxa, we feel that it would be better to postpone erection of a new taxon for these specimens until more complete material comes to light.

RUSSELL et al. (1992) referred a premaxillary tooth crown, a maxillary(?) tooth and a partial quadrate to cf.

Lesothosaurus sp. and used this referral to support an Early Jurassic age for the La Quinta Formation. However, *Lesothosaurus* cannot be diagnosed on the basis of unambiguous synapomorphies, although it can be distinguished from all other ornithischians on the basis of a unique combination of character states (BUTLER 2005). While the material described by RUSSELL et al. (1992) exhibits a number of ornithischian symplesiomorphies (e.g. sub-triangular crown in labial view, presence of coarse marginal denticles), it is not adequate to support referral to *Lesothosaurus*. Moreover, neither the description nor the illustration of the maxillary(?) tooth provided by RUSSELL et al. (1992) records the presence or absence of a 'cingulum'. Presence of the latter character state is now regarded as the only dental synapomorphy that can be used reliably to identify isolated ornithischian teeth, due to the recent realisation that teeth from other Mesozoic archosaurs can be exceptionally similar to those of ornithischians (e.g. DZIK 2003; PARKER et al. 2005; IRMIS et al. 2007). It is possible that the maxillary(?) tooth described by RUSSELL et al. (1992) is referable to the same ornithischian taxon as the teeth described herein, but it is not possible to ascertain this on the basis of the data presented by these authors. Consequently, we are unable to confirm the ornithischian status of the RUSSELL et al. (1992) material and propose that it should be regarded as *Archosauria incertae sedis* until further information becomes available.

The age of the La Quinta Formation remains problematic, but the presence of a saurischian ilium that displays the primitive condition of a partially closed acetabulum is suggestive of either a Late Triassic or Early Jurassic age, as all post-Early Jurassic saurischians possess a fully fenestrate acetabulum. As most of the floral evidence appears to support an Early to Middle Jurassic age (SCHUBERT 1986), the presence of a primitive saurischian tends to support an Early Jurassic age for this unit. Additional work on the chrono- and biostratigraphy of the La Quinta Formation is clearly necessary if it is to be fully integrated into regional tectonic models and global palaeobiogeographical scenarios. Unfortunately, available specimens from the formation are not currently adequate for the erection of new taxa. Nevertheless, the abundance and quality of the material that has been discovered thus far suggests that further collection effort will provide much needed information on the faunas and floras of northern South America at a critical time in the evolution of terrestrial ecosystems.

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