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Ecology, Systematics and Biogeographical Relationships of Dinosaurs, Including a New Theropod, from the Santana Formation (?Albian, Early Cretaceous) of Brazil

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Although rare, dinosaurs are well preserved in calcareous nodules of the Santana Formation (Early Cretaceous, ?Albian) of the Araripe Basin, in northeastern Brazil. So far, including only a spinosauroid and three coelurosaurs, the dinosaur fauna appears depauperate. High theropod diversity in assemblages where other dinosaurs are rare or absent is not unique to the Santana Formation. It is seen also in several other assemblages, including Solnhofen and the Maevarano Formation of Madagascar. We consider several factors, including the occurrence of intraguild predation, the possibility that small theropods could subsist in marginal environments, and reliance on coastal resources, that may have been responsible for this apparent ecological imbalance. A new coelurosaur from the Santana Formation, here formally named *Mirischia asymmetrica*, is shown to be distinct from *Santanaraptor placidus* [Kellner, A.W.A. (1999) "Short note on a new dinosaur (Theropoda, Coelurosauria) from the Santana Formation (Romualdo Member, Albian) northeastern Brazil", *Boletim do Museu Nacional, Nova Serie, Rio de Janeiro, Brasil* 49, 1–8]. Other theropods from the Santana Formation are briefly reviewed. *Mirischia* is a compsognathid, more similar to the European *Compsognathus* than to the Asian *Sinosauropteryx*.

Keywords: Dinosaur; Theropoda; Compsognathidae; *Mirischia*; Brazil; Santana Formation

INTRODUCTION

The calcareous nodule bearing Romualdo Member of the Santana Formation, in the Araripe Basin of northeastern Brazil, is the world's première source of Early Cretaceous pterosaurs. It has yielded a diverse and exceptionally well preserved assemblage (Martill and Unwin, 1989; Kellner and Tomida, 2000). It is less well known that this deposit also produces rare dinosaur remains (Campos and Kellner, 1991; Frey and Martill, 1995; Kellner, 1996a). Crocodyliforms and turtles also occur (Gaffney and Meylan, 1991; Martill, 1993; Hirayama, 1998), but these are rare. Perhaps surprisingly, the initial discovery of these tetrapod remains was an incidental result of commercial excavation of Romualdo nodules for their abundant and diverse fossil fishes. Previously, artisan fossil diggers had disposed of tetrapod remains which they considered to be of little or no commercial value. Since the 1980s this situation has changed. Now, tetrapod-bearing nodules, even those containing isolated or fragmentary elements, have begun to attract high prices.

Several nodules containing dinosaur remains have been documented, although not all have been described in full, as noted by Kellner (2001). Complete skeletons have not yet been reported, but partial skeletons in exceptional states of preservation are known (Kellner, 1996a,b; Martill *et al.*, 2000). Bones within the nodules are usually preserved in three-dimensions, without flattening, sometimes in articulation (Martill *et al.*, 2000). Soft tissue preservation has been reported (Kellner, 1996a,b; 1999) and gut contents were discovered in the theropod specimen described here (Martill *et al.*, 2000).

The dinosaur fauna of the Romualdo Member is incompletely known, due to the small data set so far available, but the assemblage is clearly dominated by theropods. The first report of a non-crocodyliform, non-pterosaurian archosaur from the nodules was an isolated bone, tentatively identified as an ornithischian ischium (Leonardi and Borgamanero, 1981). This identification is

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doubtful; Kellner (1996a; 1999) treated the specimen as Dinosauria *incertae sedis*. To date, this specimen is the only indication that ornithischians may be represented in the Santana dinosaur assemblage. However, apparently undiagnostic dinosaur material has also been reported by Campos (1985).

More readily identifiable remains were figured by Campos and Kellner (1991) in a short review of the Santana Formation dinosaurs. These authors figured, but did not describe, a number of new specimens. Beginning in the mid-1990s, several theropods were reported and described. Among the first of these was the partial sacrum of a coelurosaur, described by Frey and Martill (1995). They suggested, on the basis of its pleurocoelous centra, that it had affinities with Oviraptorosauria. With respect to this identification, Makovicky and Sues (1998) noted that pleurocoelous sacral centra occur in theropods other than oviraptorosaurs. They argued that the dorsally arched long axis and expanded intercentral articulations of the Santana specimen suggest that it is not an oviraptorosaur. Although there may be insufficient grounds, at present, to refer this sacrum to Oviraptorosauria with any degree of certainty, it does resemble the sacrum of the caenagnathid *Chirostenotes* (Currie and Russell, 1988; Sues, 1994). The main difference between them is the absence of a neural spine lamina in the Santana specimen. The suggestion that the Santana specimen represents an alvarezsaurid (Marjanovic, 2000) is without foundation. This specimen lacks the distinctive transversely compressed, procoelous sacral centra that are characteristic of that group.

The first named Santana theropod, *Irritator challengeri*, was described by Martill *et al.* (1996) on the basis of a partial skull, missing the end of its snout. *Irritator* was initially referred to Bullatosauria, a group erected by Holtz (1994) to include troodontids and ornithomimosaurs, but not supported as monophyletic by more recent analyses (Makovicky and Sues, 1998; Holtz, 2000). However, the presence in *Irritator* of straight, conical, unserrated tooth crowns patterned with vertical ridges, caudally located nares and other features indicate that it is a spinosauroid (Kellner, 1996a; Charig and Milner, 1997; Sereno *et al.*, 1998). Further preparation of this specimen has now been completed and a more detailed description was recently published (Sues *et al.*, 2002).

Kellner and Campos (1996) described a second Santana spinosauroid based only on a portion of distal rostrum; they named it *Angaturama limai*. While there is no overlap of corresponding structural elements between the holotypes of *Irritator* and *Angaturama*, they are similar in their degree of lateral compression, both possess a dorsal midline crest, and both have transversely round tooth crowns with unserrated carinae (Kellner and Campos, 1996;

personal observations). Consequently, Charig and Milner (1997) and Sereno *et al.* (1998) suggested that *Angaturama* might be a junior synonym of *Irritator*. Holtz (1998) even suggested that the distal rostrum of *Angaturama* might fit on the end, as the missing rostrum of the holotype of *Irritator*. The discovery of another Santana spinosauroid specimen has recently been announced (Kellner, 2001). This appears to be the most complete Santana dinosaur yet discovered. Reportedly, it includes a complete pelvis and sacrum, caudal vertebrae, and incomplete front and hindlimbs.

Another coelurosaur from the Santana Formation, *Santanaraptor placidus*, was described by Kellner (1999). The specimen consists of an associated partial pelvis, hindlimb elements and vertebrae. It exhibits extensive preservation of soft tissues, including muscle fibres (Kellner, 1996b). As noted by Kellner (1999), the proximodistally large, U-shaped obturator notch of *Santanaraptor* indicates that this is a maniraptoriform coelurosaur. However, contra Kellner (1999; 2001), this character is not diagnostic for *Santanaraptor*. Similar ischial obturator notches are widely distributed among other maniraptoriforms, including oviraptorosaurs and deinonychosaurs. Similarly, the foramen on the base of the lesser trochanter, regarded as diagnostic for *Santanaraptor* by Kellner (1999), is not unique to this taxon (Naish, 2000). Other diagnostic characters of *Santanaraptor* have been recognized, however, so we agree that this is a distinct, diagnosable taxon. Kellner (2001) has recently suggested inclusion of *Santanaraptor* within Tyrannoraptora, a maniraptoriform group erected by Sereno (1999) to include tyrannosauroids, oviraptorosaurs and paravians. This assignment is based on the unfooted distal ischium of *Santanaraptor*. However, the polarity of this character is undetermined at present, as argued by Holtz (2000). It is possible that the ischial foot was lost several times in the evolution of maniraptoriforms. It is also clear from conflicting coelurosaur phylogenies that Sereno's (1999) groupings are controversial and at odds with results of other studies (Makovicky and Sues, 1998; Padian *et al.*, 1999; Holtz, 2000).

Martill *et al.* (2000) described another small coelurosaur from a Santana Formation nodule. In this specimen, the nearly complete pelvis, both femora, proximal parts of a tibia and fibula and several gastralia are preserved in articulation. In addition, the specimen included material filling the gut and a post-pubic air sac may be preserved. The osteology and soft tissues of this specimen were described by Martill *et al.* (2000), but it was not named, and neither its palaeoecological nor phylogenetic significance was discussed.

This specimen clearly represents a taxon, named here as a new genus and species, that is distinct from both previously described Santana coelurosaurs.

The excellent preservation and intriguing osteology of this specimen have caused it to become integral to our understanding of theropod pelvic and hindlimb morphology (Hutchinson, 2001a,b), soft tissue biology and physiology (Paul, 2001) and the interpretation of less complete remains representing similar taxa (Naish *et al.*, 2001).

Why Only Theropods?

The Santana Formation's dinosaur assemblage is unusual in that only theropods have been recorded. There is evidence that ornithopods may have been present in northeastern Brazil during the Early Cretaceous. Footprints from the Rio de Peixe Basin of Paraiba, some 100 km to the north-east of the Araripe Basin, have been attributed to hypsilophodontids (Leonardi, 1987; Leonardi *et al.*, 1987).

The Romualdo Member was deposited under brackish or quasi-marine conditions. It represents either a lagoonal setting or a basin with only restricted connections to waters of normal marine salinity (Maisey, 1991; Martill, 1993). The dinosaur fauna is allochthonous and may have been derived from nearby shoreline environments. Transport distances are likely to have been in the order of tens of kilometres or less. The distance from Santana do Cariri to the nearest mapable shoreline is about 13 km. We infer that all the dinosaur fossils represent remains of drifting carcasses, derived from the shoreline or swept out to sea from the mouths of rivers.

The environment surrounding the Araripe Basin is generally considered to have been arid or semi-arid. Thick sequences of evaporites occur in the Ipubi Formation, immediately below the Santana Formation. By far the most abundant fossils in the concretions of the Romualdo Member are fishes; several mass mortality horizons are recorded (Martill, 1988a; 1993). The flora consists largely of plants of a xerophytic nature. It is dominated by the gymnosperm *Brachyphyllum*, which had succulent leaves, and cycadiales (Crane and Maisey, 1990). The local terrestrial environment appears to have been sparsely vegetated and thus unable to support large numbers of herbivores. In these circumstances, predatory theropods would have been able to gain sustenance by scavenging along the shoreline, as well as by foraging in shallow water. It has been suggested that the spinosauroid *Baryonyx* was at least in part piscivorous (Charig and Milner, 1997). If this was so, it is equally plausible that the Santana spinosauroid *Irritator* was also facultatively piscivorous. We favour the view that *Irritator* was a generalist carnivore, preying on aquatic and terrestrial vertebrates as well as carrion, around the shoreline of the Santana lagoon. Theropods scavenging at the shoreline and fishing in shallow water

would have stood a far greater chance of being incorporated into the Santana sediments than any herbivores feeding in the hinterland.

There are other dinosaur assemblages that are notable for their abundance of theropods relative to herbivorous taxa. The extreme case is that of the Solnhofen Limestone (Kimmeridgian-Tithonian), in which the only dinosaurs preserved are the small theropods *Archaeopteryx*, *Wellnhoferia* (Elzanowski, 2001), *Compsognathus* and an unnamed form (Viohl, 1999). The Aptian/Albian to Cenomanian dinosaur-bearing sequences of North Africa yield more theropod remains than herbivores, although quantitative data are not available (Russell, 1996). In the Grès Rouges of Tafilalt, Morocco, theropods outnumber sauropods and ornithischians are absent, with the exception of a possible stegosaur (Russell, 1996). In the Wadi Milk Formation of Sudan, iguanodontids and hypsilophodontids are present but they appear to be rare compared with theropods and sauropods (Rauhut, 1999). In both the Maevarano Formation (Maastrichtian) of Madagascar and the Sao Khua Formation (Lower Cretaceous) of Thailand, the dinosaur assemblages are likewise dominated by theropods and sauropods (Sampson *et al.*, 1998; Buffetaut and Suteethorn, 1999; Krause *et al.*, 1999), while ornithischians are absent. The Santana dinosaur assemblage differs from those of Tafilalt, Sudan, Madagascar and Thailand in that no herbivores have yet been recorded. In this respect, it recalls the Solnhofen fauna.

A number of speculative scenarios have been advanced to explain the diversity of theropods in some of these faunas. Russell (1996) suggested that the Tafilalt deposit represents a trophically controlled assemblage, in which fish represented the primary food source for theropods. High theropod diversity might be explained by the presence of a large top predator, such as *Carcharodontosaurus*, which was able to take large prey that were otherwise unavailable to smaller theropods (cf. Rauhut, 1999). Diverse carnivores can coexist in the same environment, exploiting a paucispecific prey assemblage. A modern analogue is provided by African flamingo colonies, consisting of one or two prey species (*Phoenicopterus ruber* and *Phoeniconaias minor*), that are exploited by as many as nine predator species. These include falconiforms, larids, ciconiids, canids and hyaenids (Ogilvie and Ogilvie, 1986). Intraguild predation among carnivores can also increase predator diversity. It is well documented in extant carnivorans (Palomares and Caro, 1999). Intraguild predation may well have existed among theropods and could partly explain their diversity in paucispecific assemblages. Theropod abundance in an otherwise paucispecific assemblage may in some cases be due to an abundance of carrion. It is conceivable, for example that fish and

pterosaur corpses were abundant on the Solnhofen and Santana shorelines after storm events.

A possibility worth considering is that theropods may be over-represented in marine or lagoonal deposits because their size, which was often small, and their pneumatic skeletons allowed their carcasses to float and drift for longer times than those of other dinosaurs. However, this hypothesis is contradicted by the presence in many marine deposits of non-theropod dinosaurs that outnumber theropods in the number of taxa represented (see below).

The fact that compsognathid theropods are found in both the Santana and Solnhofen Formations suggests that members of this group were specifically adapted to inhabit semi-arid environments. Compsognathids may have been ecologically similar to some varanid lizards, such as *Varanus griseus* (see Kirschner *et al.*, 1996), in being opportunistic carnivores that also consumed some vegetation. The preservation of gut and stomach contents in some vertebrate fossils from the Santana Formation (Wilby and Martill, 1992) holds out the hope that this may be a testable hypothesis (cf. Munk and Sues, 1993).

SYSTEMATICS

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1887
THEROPODA Marsh, 1881
COELUROSAURIA Huene, 1914
COMPSOGNATHIDAE Cope, 1875

Genus *Mirischia* gen. nov.

Type species: *Mirischia asymmetrica* gen. et sp. nov. (Text–figures 1–9)

Derivation of name: *Mirischia*, Mir, Latin, wonderful; Ischia, Greek, pertaining to the pelvis (and not the ischia alone).

Holotype: SMNK 2349 PAL

Locality: Region of Araripina (exact locality unknown), Chapada do Araripe, Pernambuco, northeastern Brazil.

Horizon and age: Romualdo Member of the Santana Formation, Araripe Group. Lower Cretaceous (Martill and Wilby, 1993). A ?late Albian age is inferred by Pons *et al.* (1990).

Material: The holotype is the only known specimen. Prior to preparation, one dorsal vertebral centrum with part of the neural arch, four sacral vertebral centra with parts of neural arches, several gastralia and lithified contents of the terminal part of the intestinal tract, an articulated pelvis and proximal parts of the hind limbs including partial left and right ilia, left and right ossa pubis, slightly damaged left and right ischia, partial left and right femora, the proximal end of a right tibia, and the proximal end of a right fibula were contained in a single calcium carbonate concretion.

Diagnosis: *Compsognathus*-like compsognathid coelurosaur, probably reaching larger adult body size than other compsognathids, pubic peduncle of ilium with concave cranial surface, pubic boot with no cranial expansion and 32% total length of pubis, pedicular fossae located craniodorsal to neural canal on caudal dorsal vertebra, distal tips of the neural spines between 63% and 67% longer than their bases, ventral surface of sacral centra bearing shallow median depressions at either end, and extremely thin bone walls to all known elements. For a complete description see Martill *et al.* (2000).

BRIEF ANATOMICAL DESCRIPTION

Vertebral Column

Five articulated vertebrae are known for *Mirischia*, including a partial dorsal, a dorsosacral, and three sacrals, the most caudal of which is incomplete (Figs. 1–3). The vertebrae all retain distinct neurocentral sutures. Most of the cranial half of the dorsal vertebrae is missing; on its right side, a short rib in articulation with its transverse process is preserved. Pedicular fossae are located dorsal to
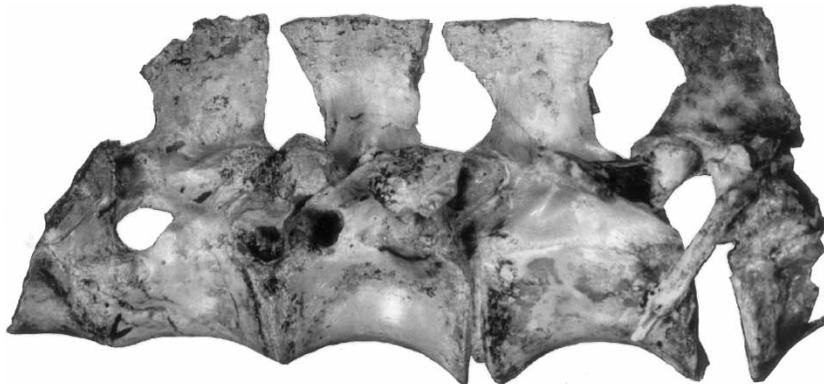

FIGURE 1   Preserved dorsal, dorsosacral and cranial sacral vertebrae of *Mirischia asymmetrica* in right lateral view. Magnification × 3.
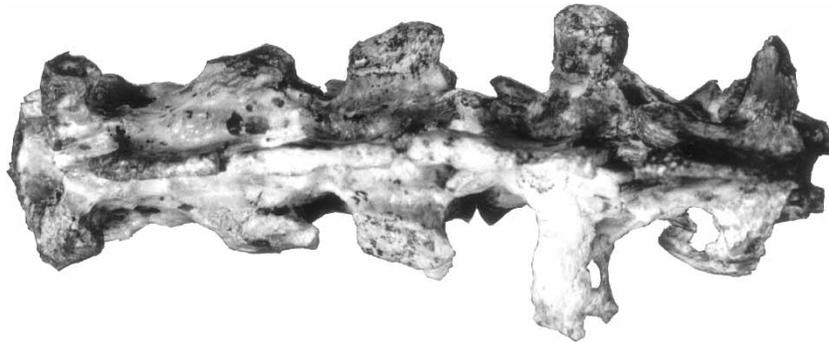
FIGURE 2   Preserved dorsal, dorsosacral and cranial sacral vertebrae of *Mirischia asymmetrica* in dorsal view. Magnification × 3.

the neural canal on the cranial surface of this vertebra (Fig. 3). That on the left is a foramen linked to the pneumatic interior of the neural arch while that on the right is a fossa. The intervertebral articulation between the second and third vertebrae remains unfused, hence the identification of the second as a dorsosacral (Martill *et al.*, 2000). The sacral vertebrae are fused and belong to the cranial part of the sacrum, the total length of which is unknown.

The sacral vertebrae of *Mirischia* are amphicoelous. On the ventral surface of each there are both parallel striations that run the length of the centrum and shallow depressions located cranially and caudally along the midline. On the second sacral vertebra, the caudal depression continues onto the ventral surface of the third centrum. To our knowledge, such depressions have not been reported in any other theropod. The more extensive ventral sulcus seen on

FIGURE 3   Preserved vertebrae of *Mirischia asymmetrica* in cranial view. Note the pedicular fossae dorsolateral to the neural canal. Magnification × 3.4.

the sacral vertebrae of eumaniraptoran coelurosaurs is clearly different.

The neural spines of *Mirischia* are cranially and caudally concave, such that the apex of the spine is between 63% and 67% longer than the base (Fig. 1).

Pelvis

The pelvis is nearly complete, with both ossa pubis, both ischia and parts of both ilia present. The distal ends of the ischia are missing, as are the caudal-most portions of both ilia. The right ilium is better preserved than the left. The width of the pelvis shows that *Mirischia* had a very narrow body, being approximately 30 mm wide across the sacrum. The preacetabular process of the ilium terminates in a square-ended process that is directed cranioventrally. The ventromedial part of this process is slightly angled laterally with respect to the dorsomedial part (Fig. 4). The ventral surface of the pubic peduncle is convex craniocaudally, with a shallow longitudinal groove; the peduncle is directed cranioventrally and it has a concave cranial margin. A cranially concave pubic peduncle also occurs in the Tyrannosauroidea. However, since there is no indication that *Mirischia* is a member of that clade, we here regard this character as a diagnostic feature of *Mirischia*. The pubis forms a long (145 mm) and slender shaft, the distal end of which forms a large pubic boot (Figs. 5 and 6). The length of this boot (53 mm) extends 37% of the length of the pubic shaft. Proximocaudally, the pubis bears a caudally projecting rectangular flange. The angle between the long axis of the sacrum and the pubis is approximately 55°.

Mirischia is remarkable in that it has an obturator foramen on the caudally projecting rectangular flange of the right pubis, but a ventrally open notch in the corresponding position on the left pubis (Martill *et al.*, 2000). Conjoined medial laminae of both ossa pubis together form a transverse pubic apron that extends from the proximal third of the pubis to the pubic boot (Fig. 7). An elongate pubic

FIGURE 4 Preserved fragment of right ilium of *Mirischia asymmetrica* in medial (A, above) and lateral (B, below) views. Magnification × 1.5.

foramen is present distally and divides the cranial third of the boot. As noted by Hutchinson (2001a), Martill *et al.* (2000) proposed that this foramen may have accommodated a ventral pneumatic duct, leading to a post-pubic air sac (Fig. 8).

The ischia of *Mirischia* are asymmetrical, that on the left being perforated by an oval foramen while that on the right has an open notch in the same position. The obturator flange on the right side is similar in shape to those of *Sinosauropteryx prima* (Currie and Chen, 2001) and *Allosaurus fragilis* (Pérez-Moreno *et al.*, 1999). The caudal margin of the ischium in *Mirischia* is evenly concave. The angle between the pubis and ischium is approximately 60° (Figs. 5 and 6).

Femur

The femur of *Mirischia* exhibits a craniodorsally curved shaft, a medially directed head set off at a right angle to the shaft, and a bifid, craniodorsally directed trochanter that is well separated from and distal to the head (Fig. 9). Most of the distal condyles are missing. Although the bifid trochanter was identified by Martill *et al.* (2000) as the lesser (or anterior) trochanter, it probably represents a fused accessory and lesser trochanter (Hutchinson, 2001b). Two small convexities caudolateral to the lesser trochanter were interpreted by Martill *et al.* (2000) as the insertion points of *m. obturatorius* and *m. iliotrochantericus*. Hutchinson (2001b) has suggested that this area represents a reduced trochanteric shelf and the attachment area for *m. iliofemoralis externus*. The fourth trochanter in *Mirischia* is a low ridge, located within the proximal third of the caudal surface of the femur.

Tibia

The right tibia is represented only by its proximal end. A shallow sulcus separates the cranial surface of the lateral condyle from the proximal third of the cnemial crest. The proximal condyles differ in shape, as is typical for theropods; the medial condyle is craniocaudally longer and mediolaterally wider than the lateral condyle. The two condyles are separated by a shallow flexor fossa. Only the proximal part of the fibular crest is preserved.

FIGURE 5 Pubis and ischium of *Mirischia asymmetrica* in right lateral view. Note enclosed foramen on proximal pubis and ventrally open obturator notch on ischium. Magnification × 1.2.

In distal cross-section, the shaft of the tibia is subtriangular.

Fibula

The right fibula is also represented only by a proximal fragment. On its medial surface, this bears a deep, parallel-sided sulcus. This is separated by a raised area from a more caudally situated depression (Fig. 10).

COMPARISONS

Mirischia closely resembles compsognathid theropods from the Late Jurassic of Europe (*Compsognathus longipes*) and the Early Cretaceous of Europe (*Aristosuchus pusillus*) and China (*Sinosauropteryx prima*) (Bidar *et al.*, 1972; Ostrom, 1978; Chen *et al.*, 1998; Naish *et al.*, 2001; Currie and Chen, 2001). However, it has proven difficult to find convincing derived characters that unite compsognathids, setting them apart from all other theropods. Currie and Chen (2001) suggested the presence of a proportionally large skull, unserrated premaxillary but serrated maxillary teeth, slender cervical ribs, short forelimbs, limited cranial expansion of the pubic boot, a prominent ischial obturator process, fan-shaped dorsal neural spines, a prominent ulnar olecranon process and a powerful manual phalanx I-1 as characters indicating a monophyletic Compsognathidae. However, they noted that some of these characters are widely distributed within Theropoda. Pending further study we provisionally accept compsognathid monophyly, regarding neural spines on the dorsal vertebrae that are craniocaudally

FIGURE 6   Pubis and ischium of *Mirischia asymmetrica* in left lateral view. Note the absence of the enclosed foramen present on the right pubis and the enclosed obturator foramen on the ischium. Magnification × 1.2.

longer at the dorsal apex than at the base ("fan-shaped" of Chen *et al.*, 1998) and limited cranial expansion of the pubic boot (Martill *et al.*, 2000; Naish *et al.*, 2001) as diagnostic features indicating membership of this group (Fig. 11).

Like *Sinosauropteryx*, *Mirischia* exhibits "fan-shaped" neural spines. This character is also seen in the dorsal neural spines of ornithomimosaurs, where the spine may be 55% longer at its tip than at its base (Makovicky, 1995). It is also reported in a basal troodontid, *Sinovenator changii* (Xu *et al.*, 2002). The distal expansion of the neural spines appears greater in *Mirischia* than in other compsognathids and ornithomimosaurs. The neural spines of *Mirischia* are between 63% and 67% longer at their distal tips than at their bases. Since compsognathids, ornithomimosaurs and troodontids are almost

certainly not close relatives (Holtz, 2000; Xu *et al.*, 2002), it appears likely that any feature which is held in common among these groups represents convergence. Distal expansion of the neural spine therefore stands as a possible compsognathid character. However, we note that ossification of the dorsal tip and of the cranial and caudal surfaces of the neural spine may vary during ontogeny. "Fan-shaped" neural spines may yet prove to be more widespread among theropods than has so far been recognized.

A prominent pubic boot with only moderate cranial expansion is present in *Mirischia*, *Compsognathus*, *Sinosauropteryx* and *Aristosuchus*. This could also be a derived compsognathid character. However, similar boot morphologies occur in other coelurosaurs (Currie and Chen, 2001), and it is difficult to quantify this character. We here compare

FIGURE 7 Conjoined ossa pubis of *Mirischia asymmetrica* in cranial view with intestinal infill preserved between the pubes. Magnification × 2.4.

Mirischia directly with the other compsognathid taxa and with the contemporaneous coelurosaur *Santanaraptor* (Kellner, 1999).

Sinosauropteryx prima

The holotype of *Sinosauropteryx prima* and at least one of the referred specimens (NIGP 127587) exhibit the same derived forelimb characters, including the proximomedial flange on the first metacarpal (Currie and Chen, 2001). Hence, we provisionally regard NIGP 127587 as a representative of *S. prima*. A third

FIGURE 8 Conjoined ossa pubis and ischia of *Mirischia asymmetrica* in caudal view. Magnification × 2.4.

specimen (GMV 2124) differs from the type specimen and from NIGP 127587 in its skeletal proportions and other anatomical features. On the basis of a cladistic analysis, Longrich (2000) concluded that the type specimen and GMV 2124 might represent two unrelated taxa.

In *S. prima*, the preacetabular process of the ilium has near-parallel dorsal and ventral margins; it does
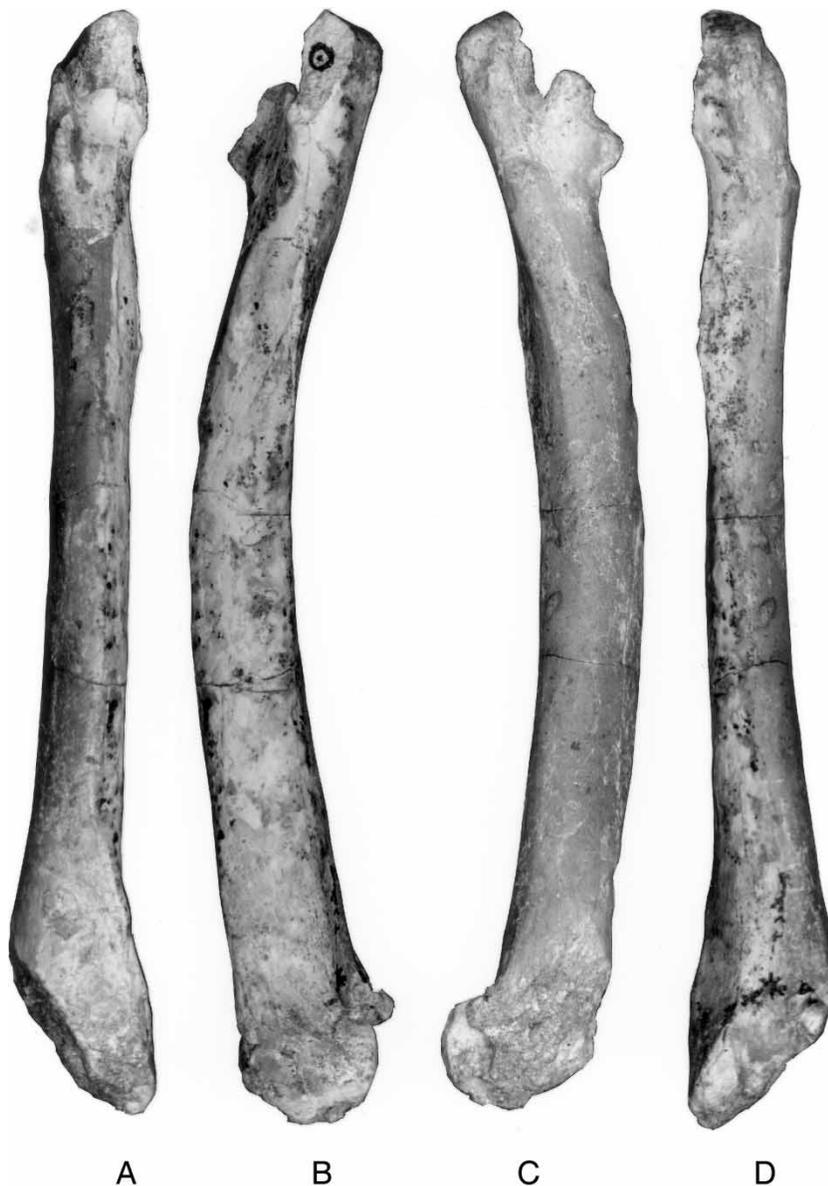
FIGURE 9   Right femur of *Mirischia asymmetrica* in A, cranial; B, medial; C, lateral; and D, caudal views. The caput is absent in these figures. Magnification × 1.1.

not exhibit marked ventral curvature at its cranial tip. In contrast, in *Mirischia* the preacetabular process curves ventrally, exhibiting a notably convex dorsal margin and a concave ventral margin. While *S. prima* has distally expanded neural spines on its dorsal vertebrae, these are not as expanded as those of *Mirischia* (Chen *et al.*, 1998). The pubic boot in *S. prima* is proportionally smaller (approximately 27% of total pubis length) than that of *Mirischia*, but the two taxa are similar in the morphology of their femora, tibiae and ischia. In *S. prima*, the lesser trochanter appears similar in form and size to that of *Mirischia*, although a distinct accessory trochanter is not evident in *S. prima* (Chen *et al.*, 1998; Currie and Chen, 2001). While in *Mirischia* and *Compsognathus* the angle between the long axis of the sacrum and the pubis is

approximately 55°, this angle is larger (about 75°) in *S. prima*, where the pubis is more vertical. This character is obviously correlated with the inclination of the pubic peduncle.

Aristosuchus pusillus

The holotype of *Aristosuchus*, long confused with *Calamospondylus oweni* (see Naish *et al.*, 2001; Naish, 2002), more resembles *Compsognathus* in the form of its pubis than any other theropod, so it is regarded as an ostensible compsognathid. The concavities and parallel striations present on the ventral surfaces of the sacral vertebrae in *Mirischia* are not present in *Aristosuchus*. The most cranial of the vertebrae in *Aristosuchus* also lacks the pedicular
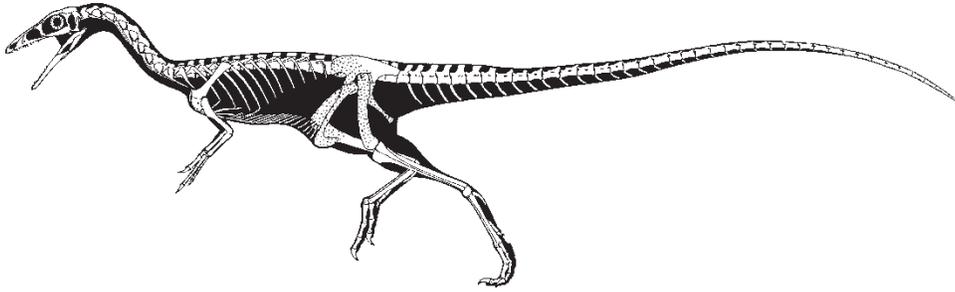
FIGURE 10 Skeletal reconstruction of the compsognathid *Compsognathus* with known elements of *Mirischia asymmetrica* stippled. Diagram by kind courtesy of Gregory S. Paul.

fossae seen on the cranial surface of the dorsal vertebra of *Mirischia*.

Two elements provisionally referred to *Aristosuchus* are strikingly similar to corresponding elements in *Mirischia*. Galton (1973) described a fragmentary proximal femur from the Wessex Formation of the Isle of Wight (specimen BMNH R5194), referring it to *Aristosuchus* (see Naish *et al.*, 2001). Like the femur of *Mirischia*, BMNH R5194 has fused lesser and accessory trochanters that exhibit a shallow V-shaped notch at their point of fusion. This morphology is probably primitive for coelurosaurs, however, and not a shared derived similarity (Hutchinson, 2001b). The reduced fourth trochanter in BMNH R5194 indicates that it is from a coelurosaur, and its similarity to the femora of *Mirischia* further suggests that it belongs to a compsognathid (Naish *et al.*, 2001). This inference is provisional in the absence of further material, however. If this specimen is from *Aristosuchus*, this taxon differs from *Mirischia* in having thicker bone walls. An isolated ischium that has provisionally been referred to *Aristosuchus* (Naish, 2002) resembles that of *Mirischia*, but differs from it in that the obturator process is triangular and thus more like the ischia of *Compsognathus*.

Compsognathus longipes

Mirischia closely resembles *Compsognathus* in having a pubic boot that lacks a cranial projection and that is almost flat ventrally. The pubic boot of *Mirischia* is virtually identical in shape to that of the Nice specimen of *Compsognathus* (Bidar *et al.*, 1972). However, the pubic boot of *Compsognathus* is proportionally larger than that of *Mirischia*. In the Nice *Compsognathus*, the length of the pubic boot is approximately 41% the total length of the shaft of the pubis (Bidar *et al.*, 1972) while in the German specimen (based on the cast BMNH R49159) it is approximately 45%. In *Mirischia*, the boot represents 32% of the total length of the pubis. There appear to be other differences between *Compsognathus* and *Mirischia*, including a triangular ischial obturator process in *Compsognathus*. However, these are

difficult to validate because of poor or incomplete preservation of skeletal material (Bidar *et al.*, 1972; Ostrom, 1978; personal observations).

Santanaraptor placidus

Mirischia is not synonymous with *Santanaraptor*. As pointed out above, *Santanaraptor* has a proportionally larger ischial obturator notch that fully separates the pubic peduncle from the obturator process (Kellner, 1999). In *Santanaraptor* the femur bears a large sulcus that is not present in *Mirischia*.

DISCUSSION: THE SANTANA DINOSAUR FAUNA

Referral of *Mirischia* to Compsognathidae has implications for the palaeobiogeographic affinities of the Santana dinosaur fauna. All previously known compsognathids are from Eurasia (Bidar *et al.*, 1972; Ostrom, 1978; Ji and Ji, 1997; Zinke, 1998; Chen *et al.*,
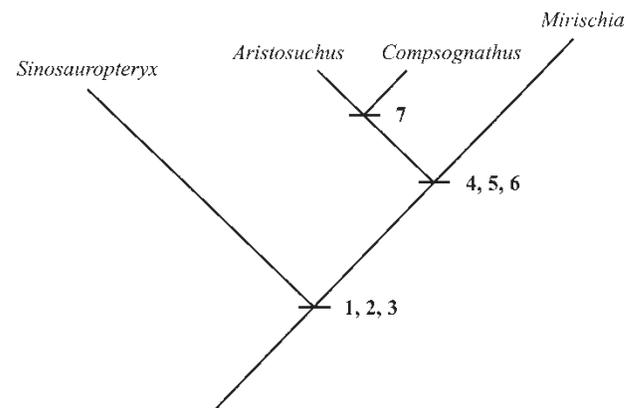

FIGURE 11 Tentative proposal of phylogenetic relationships of compsognathid taxa with compsognathid monophyly and choice of outgroups based on previous studies (Holtz, 1994; 2000). Characters defining relationships in the cladogram are as follows: (1) Unserrated premaxillary teeth; (2) Reduced/absent cranial process on pubic boot; (3) "Fan-shaped" dorsal neural spines; (4) Proportionally large pubic boot (<32% total pubis length); (5) Dorsal/sacral neural spines proportionally longer than those of *Sinosauropteryx*; (6) Angle between long axis of sacrum and shaft of pubis about 55°; (7) Triangular obturator process.

1998; Rauhut, 2000; Naish *et al.*, 2001; Currie and Chen, 2001). If compsognathids first evolved as an endemic Laurasian group, *Mirischia* constitutes evidence of an interchange of dinosaurs between Europe and South America, probably via Africa, during the Early Cretaceous. Alternatively, the geographic distribution of compsognathids may reflect vicariance following the fragmentation of Pangaea.

The referral of a theropod sacrum from the Santana Formation to Oviraptorosauria by Frey and Martill (1995) is also biogeographically significant, if this assignment proves to be correct. Thus far, there are only two other reports of members of Oviraptorosauria from Gondwana: a surangular and a dorsal vertebra from the Early Cretaceous of Australia (Currie *et al.*, 1996), and an isolated cervical vertebra from the Late Cretaceous of Argentina (Frankfurt and Chiappe, 1999).

The spinosauroid *Irritator challengeri* (Martill *et al.*, 1996) indicates that the dinosaur fauna of the Santana Formation includes elements at the suprageneric level that also are found in the Early and mid-Cretaceous of Africa. Other similarities between the Santana tetrapod assemblage and North African Cretaceous assemblages are well known (Buffetaut and Taquet, 1979; but see Kellner, 1994; Ortega *et al.*, 2000), suggesting that Eurasian dinosaurs could have spread to South America by way of Africa.

As noted above, Kellner (1999) suggested that *Santanaraptor* may belong to Maniraptoriformes. This coelurosaur clade is now well documented in the Cretaceous of South America, where it is represented by *Unenlagia*, oviraptorosaurs, alvarezsaurids and avialians (Novas, 1996; 1997; Novas and Puerta, 1997; Frankfurt and Chiappe, 1999). Maniraptoriform dinosaurs were evidently widely distributed; they appear to have had an almost global geographic range in the Cretaceous.

In conclusion, the presence in the Santana Formation of spinosauroids, compsognathids and maniraptoriforms casts further doubt on suggestions (Bonaparte, 1996) that Gondwana had a distinct, endemic tetrapod fauna during the Cretaceous.

Acknowledgements

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are known from both of these organic-rich mudrocks and, although the data sets are small, dinosaurs are represented in both cases by most of the major groups (Martill, 1988b). Similar numbers of dinosaur specimens have been recorded from these Jurassic marine mudrock formations, the Santana Formation, and the Solnhofen Limestone. Thus, it is surprising that all the approximately ten dinosaur specimens collected from Solnhofen, even after 150 years, are theropods. Similarly, we know of about eight specimens, all of them theropods, from the Santana Formation. The Oxford Clay of Peterborough, England has yielded about ten dinosaur specimens, representing seven taxa, only two of which are theropods. The Kimmeridge Clay of southern England has yielded nine taxa (total specimen count is not known) of which only two are theropods. One of these theropods is an undescribed partial skeleton. In all cases, these faunas are considered allochthonous, the dinosaurs probably having drifted into marginal marine environments from river systems draining local hinterlands. Despite the small numbers of specimens, the terrestrial environments adjacent to the Santana Formation and the Solnhofen Limestone do appear to have supported at most limited numbers of herbivorous dinosaurs.

APPENDIX: A COMMENT ON SMALL DATA SETS

The tetrapod assemblage of the Santana Formation is similar to that of the Jurassic Solnhofen Limestone, at least in terms of the reconstructed terrestrial palaeoenvironment and the presence of carnivorous terrestrial tetrapods. The hinterland of the Solnhofen lagoons, like that of the Santana lagoon, is thought to have been semi-arid (Barthel *et al.*, 1990). One might argue that this is an unusual deposit in that it represents a marine, lagoonal environment with many fossils of terrestrial origin. However, allochthonous dinosaur assemblages are well-known from several fully marine deposits, including the Callovian to Oxfordian (Middle to Late Jurassic) Oxford Clay and the Kimmeridgian (Late Jurassic) Kimmeridge Clay, both in England (Martill, 1988b). Dinosaurs

ADDENDUM

After this paper had been accepted for publication, two published studies appeared which included discussions of compsognathid systematics and phylogeny (Rauhut, 2003; Hwang *et al.*, 2004) While both employed a more thorough analysis of character distribution within Coelurosauria than the present study, both supported compsognathid monophyly and inclusion within the clade of the same taxa included here. Though Rauhut (2003) argued that the holotype of *Mirischia* should be regarded as Compsognathinae indet., he also noted that it probably represented a distinct taxon. Hwang *et al.* (2004) described the new compsognathid *Huaxiagnathus orientalis* from the Yixian Formation (probably the most basal compsognathid) and agreed that *Mirischia* is a compsognathid, albeit one too incomplete to include in their analysis.