The early evolution of postcranial skeletal pneumaticity in sauropodomorph dinosaurs

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Postcranial skeletal pneumaticity (PSP) is present in a range of basal sauropodomorphs spanning the basal sauropodomorph–sauropod transition. We describe the PSP of five taxa, *Plateosaurus engelhardti, Eucnemesaurus fortis*, *Aardonyx celestae*, *Antetonitrus ingenipes*, and an unnamed basal sauropod from Spion Kop, South Africa (hereafter referred to as the Spion Kop sauropod). The PSP of *Plateosaurus* is apparently sporadic in its occurrence and has only been observed in very few specimens, in which it is of very limited extent, affecting only the posterior cervical vertebrae and possibly the mid dorsals in one specimen. The PSP of *Eucnemesaurus*, *Aardonyx*, *Antetonitrus*, and the Spion Kop sauropod consists of subfossae (fossa-within-fossa structures) that excavate the vertices of the posterior infradiapophyseal fossae of the posterior dorsal vertebrae. These subfossae range from simple shallow depressions (*Eucnemesaurus*) to deep, steep-sided, internally subdivided and asymmetrically developed chambers (*Antetonitrus*). The middle and anterior dorsal vertebrae of these taxa lack PSP, demonstrating that abdominal air sacs were the source of the invasive diverticula. The presence of pneumatic features within the infradiapophyseal fossae suggest that the homologous fossae of more basal saurischians and dinosauriforms were receptacles that housed pneumatic diverticula. We suggest that it is probable that rigid non-compliant lungs ventilated by compliant posterior air sacs evolved prior to the origination of Dinosauria.

Key words: Sauropodomorpha, Sauropoda, postcranial skeletal pneumaticity, air-sacs, Triassic, Jurassic, South Africa.

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Introduction

Derived sauropod dinosaurs from the clade Eusauropoda are well known for their cavernous presacral vertebrae. Suggestions that these vertebrae were pneumatic were made as early as 1870, before Sauropoda were even recognised as a group (Seeley 1870). Owen (1876) however dissented and claimed that cartilage likely filled the internal chambers of these vertebrae. Strangely enough, Owen (1856) had earlier supported the idea that the external fossae of eusauropod vertebrae housed pneumatic diverticula from the lung. Despite this early start, the idea that eusauropod vertebrae were pneumatic received little scientific scrutiny until the 1990s (e.g., Janensch 1947; see Wedel 2003a). Recent detailed comparisons with modern birds (Britt 1993; Wedel et al. 2000; Wedel 2003a, b, 2005; O'Connor 2006) have confirmed that the presacral vertebrae of eusauropods were pneumatised by pulmonary diverticula.

By working from modern bird dissections Britt (1993) proposed a list of five osteological correlates of postcranial skeletal pneumaticity (PSP) in modern birds. These were: large foramina, fossae with crenulate texture, thin outer walls, broad tracks with smooth or crenulated texture, internal chambers communicating with the exterior via foramina. However, most of these features are not absolutely diagnostic. Thus diagnosis of PSP using these criteria is an exercise in probability: the greater the number of correlates present, the more likely the presence of PSP. Only foramina that open into internal chambers have been accepted as incontrovertible evidence for the presence of PSP (O'Connor 2006). However it is not necessary for PSP to take this form. Some pneumatic fossae of modern birds are simple shallow fossae that lack sharp rims (e.g., Wedel 2007: fig. 9). This fossa is taken to be pneumatic because: (i) it occupies a known site of pneumatic invasion of a diverticulum from the cervical air sac (see O'Connor and Claessens 2005: fig. 1); (ii) its counterpart on the right side of the same bone is a fully-diagnostic pneumatic foramen; (iii) no other soft tissue structure is known to excavate the dorsal surface of avian cervical vertebrae. Throughout this paper we use the position of a potential pneumatic structure on the bone sur-

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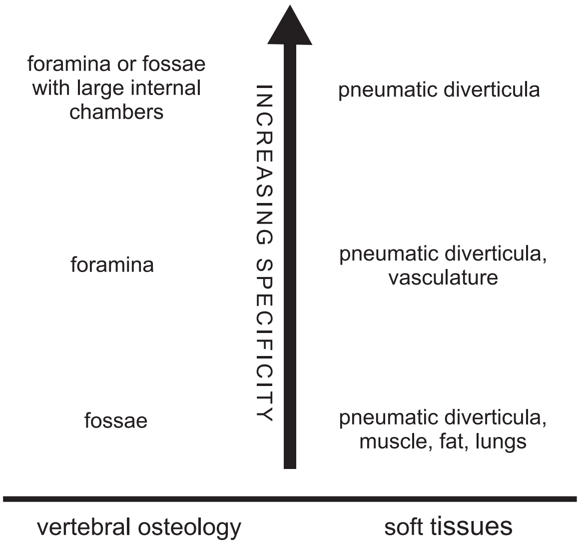

Fig. 1. The pneumaticity profile of O'Connor (2006: fig. 12). The osteological correlate with the lowest specificity is at the bottom of the profile, while the correlate that specifies only pneumatic diverticula is at the top. The profile has been modified to indicate that pneumatic diverticula can form simple vertebral fossae.

face as an additional criterion for assessing the probability that a given structure is pneumatic in origin. This is a simple usage of one of the main criteria of homology: that of position, by which primary homology assessments are made (Remane 1952). In this case the use of this criterion is bolstered by the observation that the sites of pneumatic invasion frequently repeat themselves along the length of a vertebral column within an individual as well as between individuals of different taxa. The nearly ubiquitous location of pneumatic foramina on the lateral surfaces of vertebral centra of dinosaurs with PSP is an obvious example.

O'Connor (2006) refined Britt's (1993) list of correlates and produced a profile of osteological characters that are correlated with increasingly specific soft tissue structures (Fig. 1). At the base of the profile are simple vertebral fossae, which may house muscles, fat bodies or lung diverticula. Interestingly O'Connor (2006) did not list pneumatic diverticula as one of the soft tissue structures capable of forming vertebral fossae but, as mentioned above, they certainly are. Fossae and foramina that open into internal chambers are placed at the top of O'Connor's (2006) "pneumaticity profile" since pneumatic diverticula are the only known soft-tissue structures known to produce them. All but the most basal of Eusauropoda have internal vertebral chambers communicating with the exterior via fossae and foramina and thus the inference that they have PSP is strong despite the fact that only one side of their extant phylogenetic bracket (birds) has PSP, i.e., it is a level II inference of soft tissue structure in a fossil taxon (Witmer 1997). Although O'Connor's pneumaticity profile is useful for identifying unambiguous PSP in extinct tetrapods it is of limited utility for examining the origin and early evolution of PSP where pneumatic features are less elaborate and therefore less diagnostic.

A number of questions now flow from this research. Namely: when did PSP evolve in Sauropodomorpha? Did pneumatic invasion of the presacral column follow the same pattern that is seen in theropod phylogeny and modern bird ontogeny? Were the initial invasion points on the vertebrae similar? What air sacs were likely to have been present and does this inform us about the evolution of avian style lungs? A more difficult, but not intractable, question is: can earlier stages of PSP be recognised even if they do not take the form of expansive internal chambers that communicate with the exterior via pneumatic foramina? In this paper we examine these questions in light of new material from South Africa that spans the basal sauropodomorph–sauropod transition.

Taxonomic definitions.—Understanding of early sauropodomorph interrelationships has been unstable in recent years and their phylogenetic nomenclature has varied from work to work. Here we define precisely the various clade names employed in this paper (Fig. 2). We use Sauropodomorpha in the sense of the stem-group sister group to Theropoda (defined as the most inclusive clade containing *Saltasaurus*

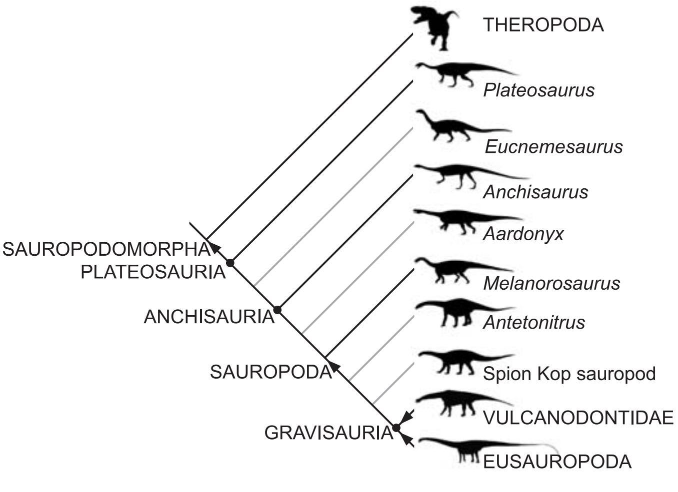

Fig. 2. A simplified cladogram of sauropodomorph dinosaurs indicating the relative positions of various anchor taxa, or their inclusive clades, other taxa discussed in the paper and the higher-level taxonomy that is used. Dots represent node-based taxa, arrows represent stem-based taxa.

Table 1. Abbreviations and the bounding laminae for the three primary infradiapophyseal fossae discussed in this paper.

Fossa	Abbreviation	Bounding lamina 1	Bounding lamina 2
anterior infradiapophyseal fossa	AIDF	prezygodiapophyseal lamina	paradiapophyseal or anterior centrodiapophyseal lamina
middle infradiapophyseal fossa	MIDF	paradiapophyseal or anterior centrodiapophyseal lamina	posterior centrodiapophyseal lamina
posterior infradiapophyseal fossa	PIDF	posterior centrodiapophyseal lamina	postzygodiapophyseal lamina

loricatus but not *Tyrannosaurus rex*; Taylor et al. in press). Anchisauria are defined as the least inclusive clade including both *Anchisaurus polyzelus* and *Melanorosaurus readi* (Galton and Upchurch 2004). In our preferred phylogeny (Yates et al. 2010) it includes *Anchisaurus*, *Aardonyx*, *Melanorosaurus* and Sauropoda. Sauropoda are defined as the most inclusive clade containing *Saltasaurus loricatus* but not *Melanorosaurus readi* (Yates 2007). Gravisauria are defined as the least inclusive clade containing *Vulcanodon karibaensis* and *Saltasaurus loricatus* (Allain and Aquesbi 2008). Within Graviasauria, Eusauropoda are defined as all those taxa sharing a more recent common ancestry with *Saltasaurus* than *Vulcanodon* (Wilson and Sereno 1998).

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; BP, Bernard Price Institute (Palaeontology), University of the Witwatersrand, Johannesburg, South Africa; BRSUG, Department of Earth Sciences, University of Bristol, Bristol, United Kingdom; GPIT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany; MB, Museum für Naturkunde der Humboldt Universität, Berlin; NHM, Natural History Museum, London, United Kingdom; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TM, Transvaal Museum, Tshwane, South Africa.

Other abbreviations.—AIDF, anterior infradiapophyseal fossa; MIDF, middle infradiapophyseal fossa; PIDF, posterior infradiapophyseal fossa; PSP, postcranial skeletal pneumaticity.

Material

The presacral vertebrae of five taxa spanning the basal sauropodomorph–sauropod transition were examined: *Plateosaurus engelhardti*, *Eucnemesaurus fortis*, *Aardonyx celestae*, *Antetonitrus ingenipes*, and the Spion Kop sauropod. Throughout the descriptions and discussion we refer frequently to “infradiapophyseal fossae”. These are the triangular spaces formed between the four primitive vertebral laminae of saurischian vertebrae that radiate from the diapophysis. There are usually three such fossae: the anterior infradiapophyseal fossa (AIDF) which is bounded by the prezygodiapophyseal and paradiapophyseal laminae although in some cases it is bounded by the prezygodiapophyseal and anterior centrodiapophyseal lamina; the middle infradiapophyseal fossa (MIDF) which is bounded by the paradiapophyseal (or anterior centrodiapophyseal lamina) and posterior centrodiapophyseal laminae; the posterior infradiapophyseal fossa (PIDF) which is bound by the posterior centrodiapophyseal lamina and the postzygodiapophyseal lamina (Fig. 3, Table 1).

Wilson (1999) drew attention to the smaller round fossae that excavate the larger fossae bound by the vertebral laminae (e.g., the infradiapophyseal fossae) of many eusauropods and labelled them “subfossae”. In this paper we use the term subfossa for any smaller hollow excavated into the wall of a larger infradiapophyseal fossa.

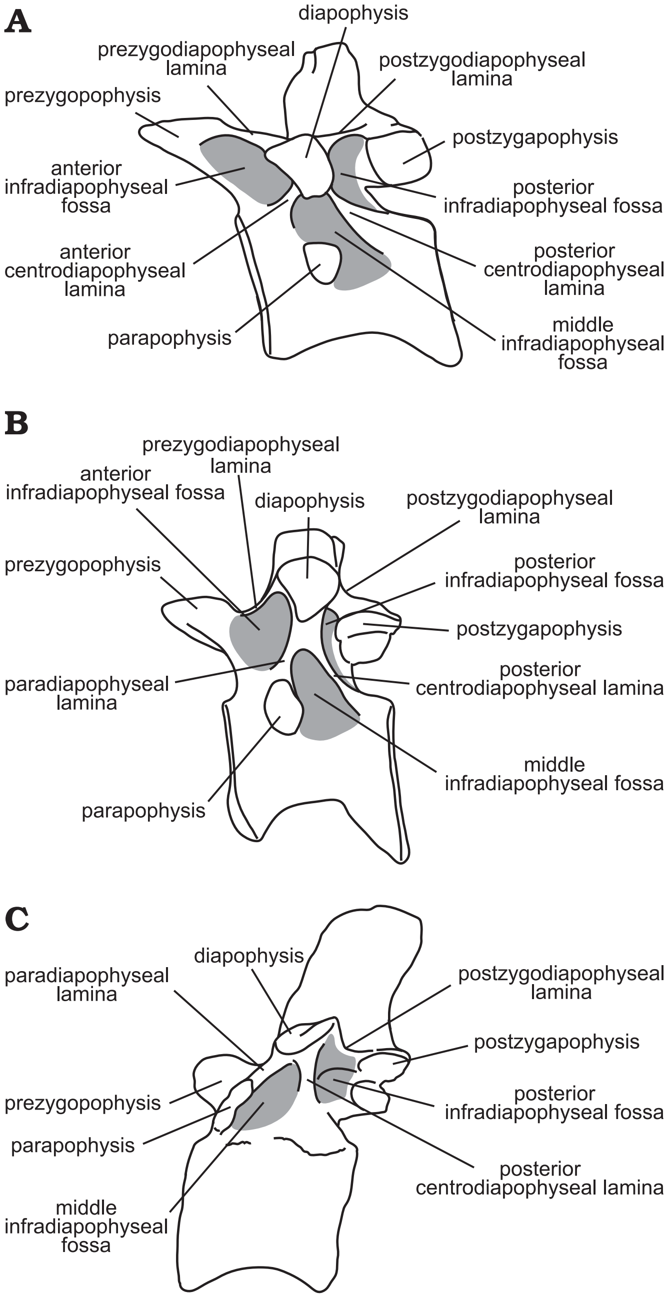

Fig. 3. Selected vertebrae of basal sauropodomorphs showing the three primary infradiapophyseal fossae (shaded grey) and their bounding laminae (not to scale). **A**. *Plateosaurus engelhardti* Meyer, 1837; C9, the posterior cervical vertebra. **B**. *Plateosaurus engelhardti* Meyer, 1837; D2, the anterior dorsal vertebra. Note that in this vertebra the central position of the parapophysis precludes the presence of a paradiapophyseal lamina and so the AIDF and MIDF are separated by an anterior centroparapophyseal lamina. **C**. *Aardonyx celestae* Yates, Bonnan, Neveling, Chinsamy, and Blackbeard, 2010, a middle posterior dorsal vertebra. Note that in this vertebra the prezygodiapophyseal lamina and the AIDF are absent. A, B redrawn from Bonaparte (1999).

Plateosaurus.—The vertebral column of the mounted skeleton AMNH 6810 was examined (Fig. 4). This specimen,which

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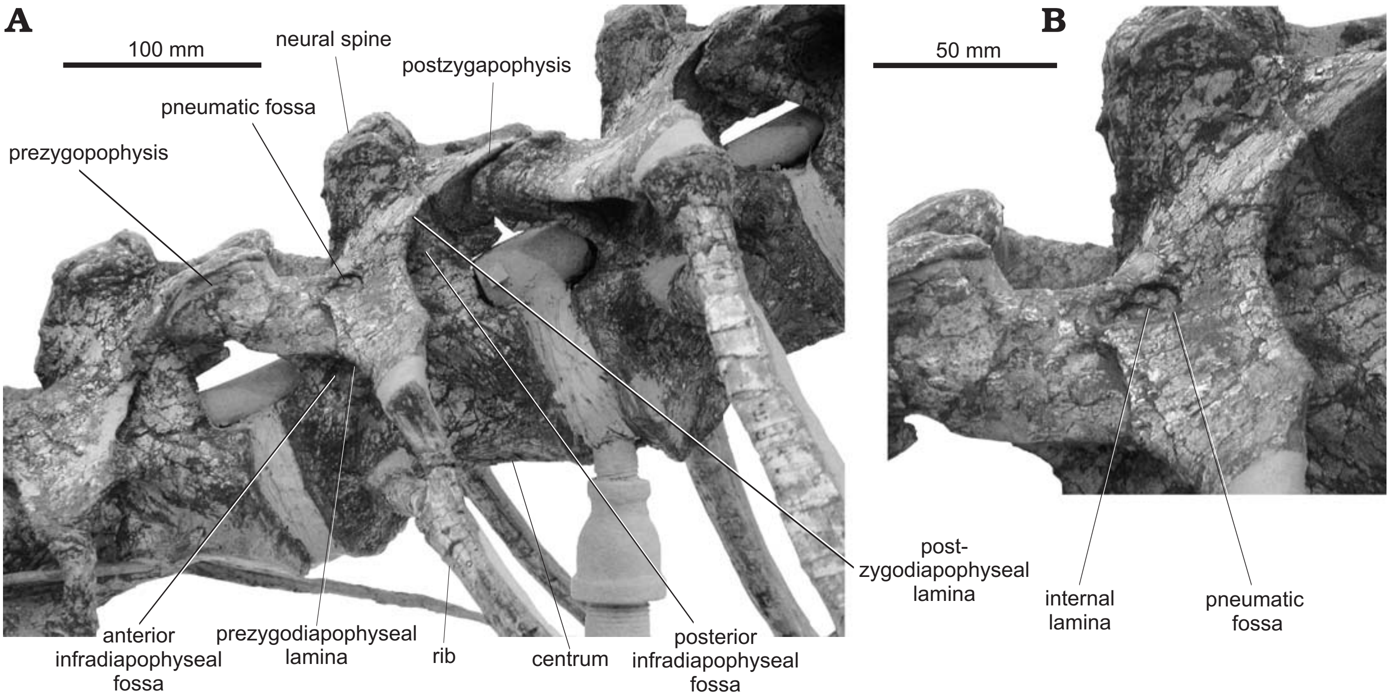

Fig. 4. Cervico-dorsal transition of the vertebral column of the basal sauropodomorph *Plateosaurus engelhardti* Meyer, 1837, AMNH 6810 from the Upper Triassic Loewenstein Formation of the Trossingen Quarry, Germany. **A**. The posterior cervical vertebrae, C9 and 10 (left and middle) and the first dorsal vertebra, D1 (right) in left lateral view. **B**. Close-up of the pneumatic fossa on the dorsal surface of C10.

we refer to *Plateosaurus engelhardti*, comes from the upper Löwenstein Formation (Norian, Late Triassic) of the famous *Plateosaurus* quarry of Trossingen, Germany. It was excavated as an articulated skeleton before preparation and mounting (Galton 2001 and references therein).

Eucnemesaurus.—This taxon derives from the Late Triassic lower Elliot Formation of South Africa. Although it has been found to form a sister group relationship with *Riojasaurus* in all analyses that have included it (e.g., Yates 2007), new, undescribed material suggests that it is a more derived taxon that is close to Anchisauria (AMY personal obserwations). We examined a single posterior dorsal vertebra of BP/1/6107 (Fig. 5A$_1$–A$_3$), a mature specimen of *Eucnemesaurus fortis* that was described by Yates (2007), and the neural arch of a middle dorsal of the holotype specimen, TM 119 (Fig. 5B). BP/1/6107 consists of fragmentary postcranial remains presumed to belong to a single individual. Unlike BP/1/6107, TM 119 is a smaller individual that has open neurocentral sutures, indicating that it was probably immature at the time of death.

Aardonyx.—*Aardonyx celestae* appears to be the sister group of the quadrupedal sauropodomorph clade which includes *Melanorosaurus* and Sauropoda (Yates et al. 2010). It is represented by a large sample of well-preserved elements. These all come from the topotypic bone bed (Early Jurassic, upper Elliot Formation of Spion Kop, South Africa) and probably belong to two immature individuals (Yates et al. 2010). The sample includes a cervical centrum (BP/1/6644), cervical neural arches (BP/1/6513, 6615, 6662, 6681; Fig. 6), anterior, middle and posterior dorsal neural arches (BP/1/6287, 6323, 6591, 6642, 6666), anterior and posterior dorsal centra (BP/1/6261, 6324, 6613) one complete posterior dorsal vertebra (BP/1/6566; Fig. 7), sacral neural arches (BP/1/5379, 6309; Fig. 8A) and one sacral centrum (BP/1/6241; Fig. 8B).

Antetonitrus.—Another taxon from the Late Triassic lower Elliot Foramation of South Africa. The dorsal neural arches of the holotype of the basal sauropod *Antetonitrus ingenipes* (BP/1/4952) were re-examined. These consist of an anterior middle dorsal, probably the fourth or fifth (Yates and Kitching 2003: fig. 3a–c); a middle dorsal, probably the seventh or eighth; a posterior middle dorsal, probably the tenth or eleventh; and a posterior dorsal, probably the thirteenth or fourteenth (Yates and Kitching 2003: fig. 3d–f). The previously unfigured middle dorsal neural arch was prepared further, revealing unexpected and rather dramatic pneumatic structures (Fig. 9). These were previously hidden behind an infilling of matrix that was itself obscured by a heavy coat of glue.

Spion Kop sauropod.—This taxon is an undescribed basal sauropod from the Early Jurassic upper Elliot Formation locality of Spion Kop that appears to be more closely related to Gravisauria than to *Antetonitrus* (AMY unpublished data). Three vertebrae were examined: an anterior cervical vertebra (BP/1/6199; Fig. 10B) from a mature individual (based on the closure of the neurocentral sutures) and two dorsal neural arches, from a smaller immature individual (BP/1/6183; Fig. 10A). The latter include a middle dorsal neural arch that has been transversely compressed by sediment compaction and a posterior dorsal that has been anteroposteriorly compressed.

Lastly the vertebral columns of several presumed apneu-

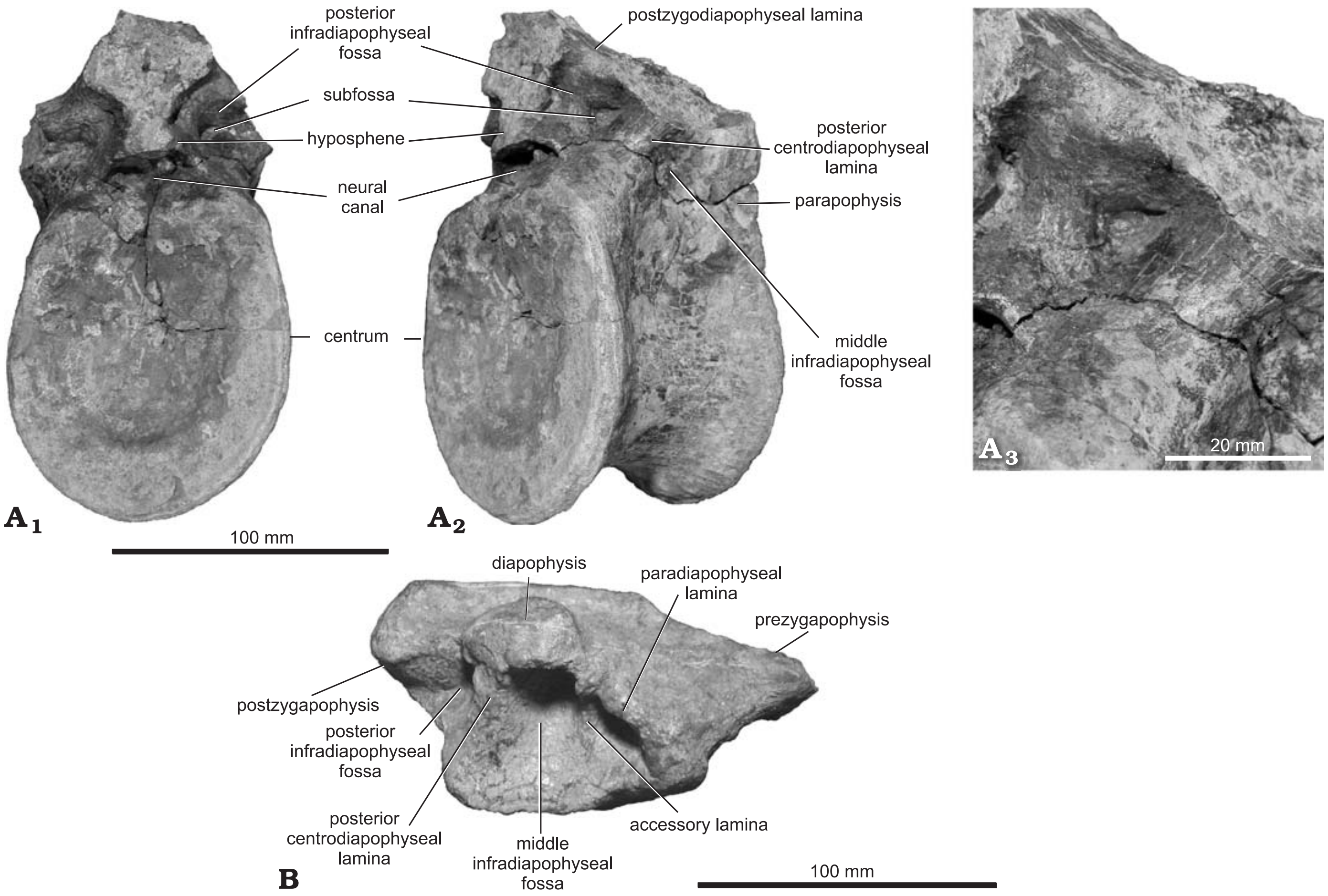

Fig. 5. Dorsal vertebrae of the basal sauropodomorph *Eucnemesaurus fortis* Van Hoepen, 1920, from the Upper Triassic Elliot Formation of South Africa. **A**. Posterior dorsal BP/1/6107 in posterior (A_1) and right posterolateral (A_2) views. Close-up of the right posterior infradiapophyseal fossa in posterolateral view (A_3). **B**. Neural arch of middle dorsal TM 119 in right lateral view.

matic basal sauropodomorph taxa were examined in order to confirm the lack of any special pneumatic features over and above the normal complement of saurischian laminae and infradiapophyseal fossae. These taxa include *Thecodontosaurus antiquus* (BRSUG 26629, 28124, 28133, 26621, 28131, 23969, 26645, 26589, 28122), *Efraasia minor* (SMNS 12354, 12684), and *Massospondylus carinatus* (BP/1/4934, 5143, 5241).

Description

Plateosaurus (Fig. 4).—The left dorsolateral surface of the neural arch of the tenth and last cervical vertebra of AMNH 6810 displays a small, round, sharp-rimmed fossa of approximately 15 mm in diameter which is divided internally by a thin oblique anterodorsal-posteroventral lamina. Vertebrae on either side lack similar fossae. A second specimen (SMNS F65) develops a pair of large subfossae (diameter reaching 10 mm) in the PIDF of one of the posterior cervical vertebrae (probably the ninth) that are separated by thin bony laminae (Richard J. Butler, personal communication 2010). Other specimens of *Plateosaurus* lack dorsal pneumatic fossa altogether (e.g., GPIT 1, SMNS 13200), although a middle dorsal of SMNS 12950 has a cluster of large foramina at the vertex of the AIDF (Richard J. Butler, personal communication 2010). Similar clusters of foramina have been reported in the basal archosauriform *Erythrosuchus* (Gower 2001; Wedel 2007) but it remains uncertain whether or not these features are vascular or pneumatic and we will not discuss them further here. Janensch (1947: 21–22) also reported a sizeable (11×4 mm), and possi-

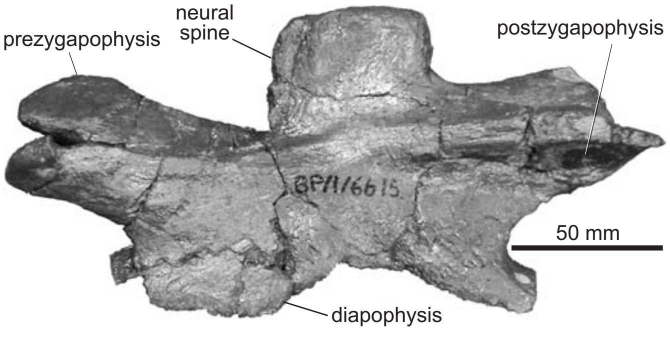

Fig. 6. Neural arch of posterior cervical vertebra, ?C7 of the basal sauropodomorph *Aardonyx celestae* Yates, Bonnan, Neveling, Chinsamy, and Blackbeard, 2010, BP/1/6615 from the Elliot Formation of Spion Kop, South Africa, in left lateral view.

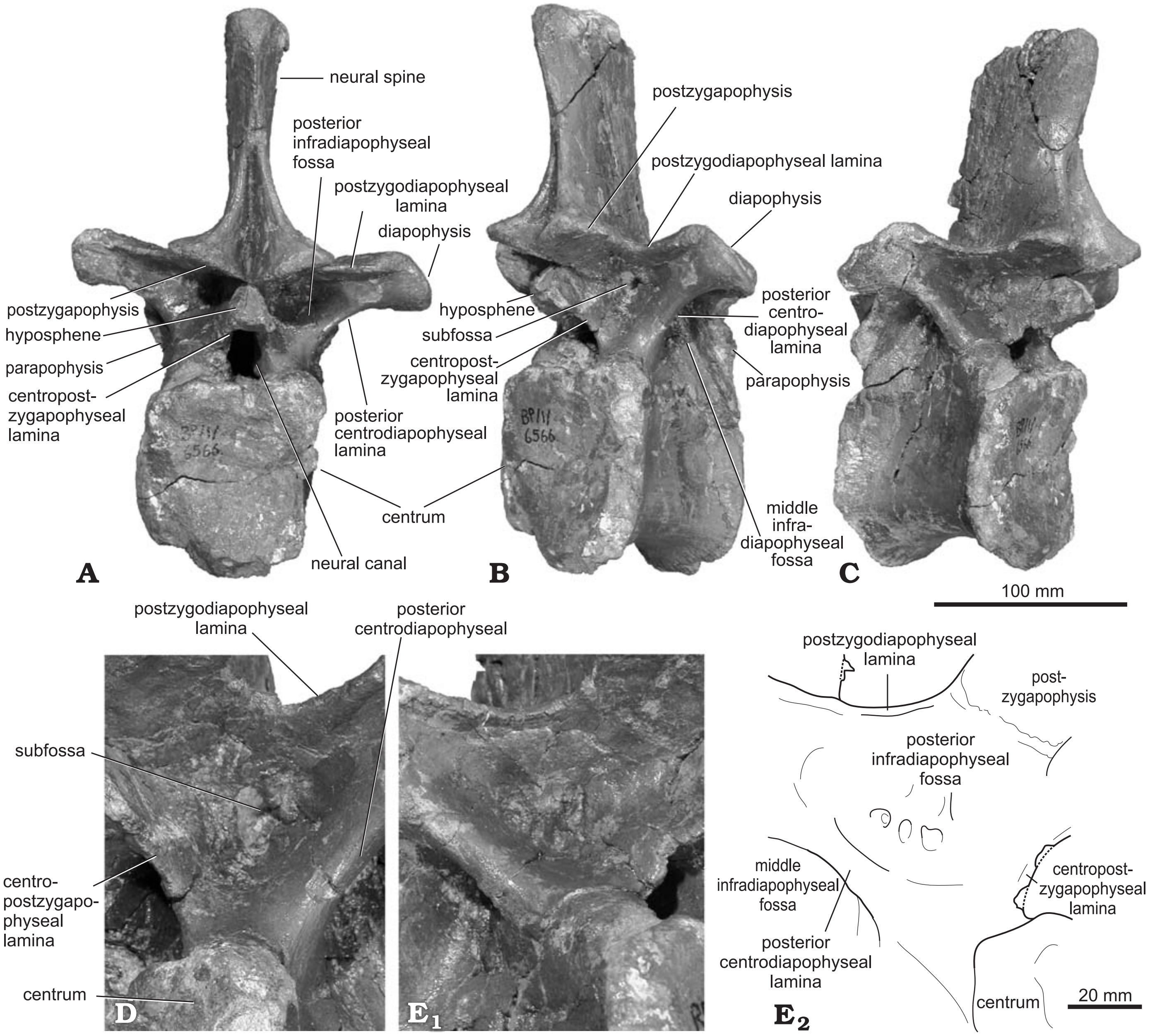

Fig. 7. Posterior dorsal vertebra of the basal sauropodomorph *Aardonyx celestae* Yates, Bonnan, Neveling, Chinsamy, and Blackbeard, 2010, BP/1/6566 from the Lower Jurassic Elliot Formation of Spion Kop, South Africa, in posterior (**A**), right posterolateral (**B**), and left posterolateral (**C**) views. Close-ups of right (**D**) and left (**E**) posterior infradiapophyseal fossae. Photograph (E_1) and explanatory drawing (E_2).

bly pneumatic, foramen in a partial dorsal vertebra (MB HMN fund IX) referred to *Plateosaurus*. The foramen is located in the left AIDF, which is bounded by the prezygodiapophyseal lamina and the anterior centrodiapophyseal laminae (this fossa was referred to by Janensch as the "Infrapräzygapophysial-nische"). Wedel (2007) raised the possibility that this foramen was vascular in origin, in part because no other good evidence for PSP in basal sauropodmorphs was known at the time. In light of our findings here, more work is needed on the morphology of the foramen, the serial position of the vertebra, and its referral to *Plateosaurus*.

Eucnemesaurus (Fig. 5).—The posterior dorsal vertebra of BP/1/6107 is typical for basal sauropodomorphs. The diapophysis is supported ventrally by two laminae: the paradiapophyseal lamina and the posterior centrodiapophyseal lamina. These two laminae bound the MIDF. A third diapophyseal lamina, the postzygodiapophyseal lamina, extends posterodorsally to the postzygapophysis. The PIDF is bounded by the posterior centrodiapophyseal lamina and the postzygodiapophyseal lamina. Yates and Kitching (2003) included in their cladistic analysis of sauropodomorph dinosaurs the presence of an accessory lamina that partially divides the PIDF as a derived character that occurs sporadically among basal sauropodomorphs. Yates (2007: fig. 3e) reported that such an accessory lamina was present in BP/1/6107. However, further preparation has shown that this presumed

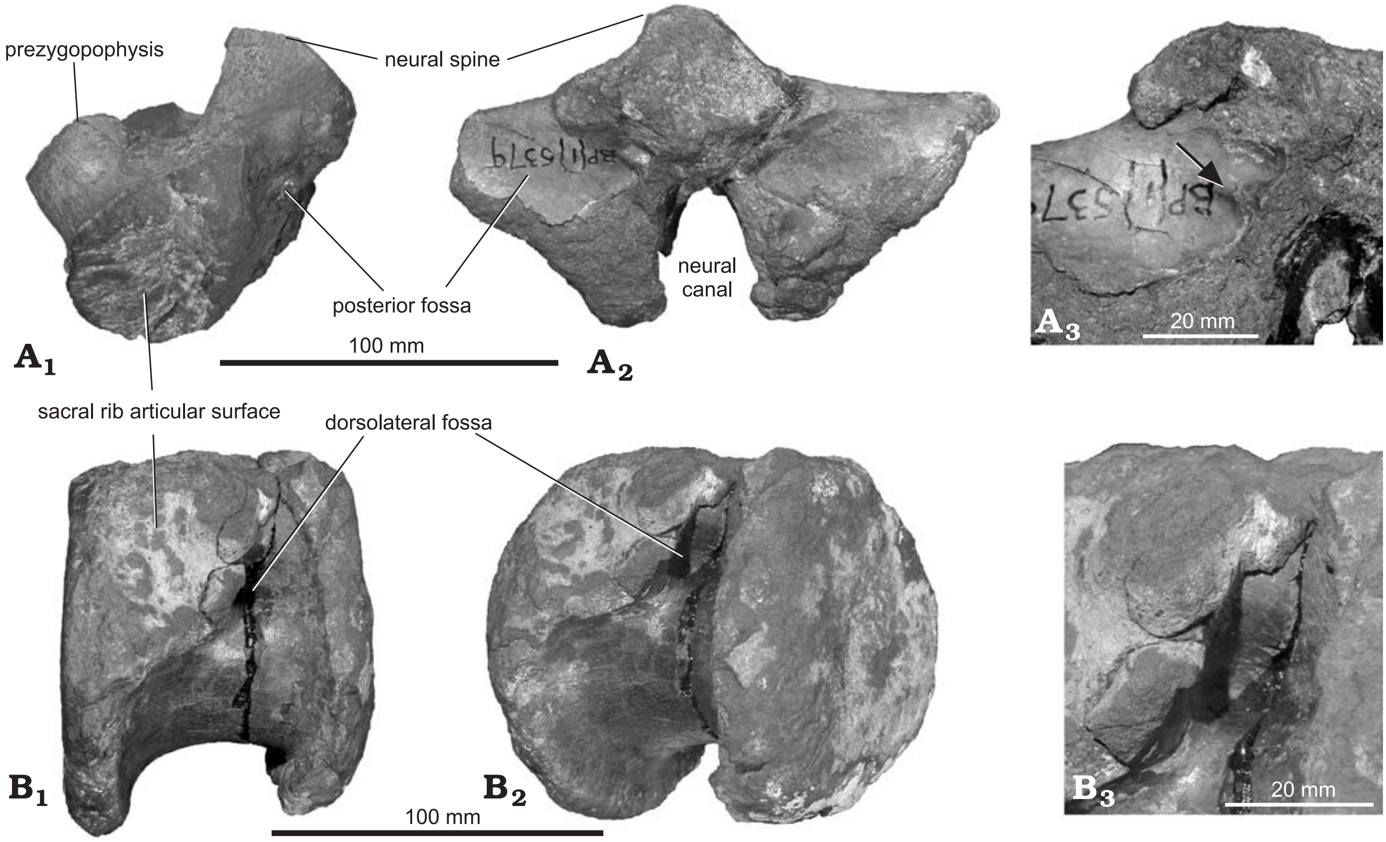

Fig. 8. Sacral elements of the basal sauropodomorph *Aardonyx celestae* Yates, Bonnan, Neveling, Chinsamy, and Blackbeard, 2010, from the Lower Jurassic Elliot Formation of Spion Kop, South Africa. **A**. Incomplete neural arch of first sacral vertebra, BP/1/5379 in left lateral (A_1) and posterior (A_2) views. Close-up of left posterior fossa in posteroventral view (A_3). Note the subfossae separated by a ridge (arrowed). **B**. First sacral centrum, BP/1/6241 in left lateral (B_1) and oblique posterolateral and slightly ventral (B_2) views. Close-up of the dorsolateral fossa (B_3) developed behind the sutural scar for the attachment of the sacral rib.

lamina was the posteromedial margin of a subtriangular subfossa that excavates the wall of the PIDF at its deepest point (Fig. 5A_3). In BP/1/6107 the subfossae are about 19 mm across, have smoothly rounded rims and are developed symmetrically with one in each PIDF. They are shallow, reaching a depth of no more than 5 mm. They are lined throughout with periosteal bone. The MIDF lacks subfossae and the lateral surface of the centrum does not bear any trace of pneumaticity either. The anterior dorsal neural arch of TM 119 does not have subfossae developed in the PIDF but does show an accessory lamina in the MIDF (Yates 2007: fig 3a; Fig. 5B). This lamina is raised above the wall of the infradiapophyseal fossa and is therefore not thought to be the result of invasion of the neural arch by pneumatic diverticula.

Aardonyx (Figs. 5–7).—The cervical neural arches and cervical centrum do not display any signs of pneumatisation. Not even the typical diapophyseal laminae and infradiapophyseal fossae are present in any of the cervical neural arches, including those thought to be from the posterior end of the series (Fig. 6). Anterior dorsal vertebrae do bear typical saurischian diapophyseal laminae and infradiapophyseal fossae, but these do not bear any sign of subfossae or other unambiguous pneumatic features developed within them.

Clearer signs of pneumatisation are found in the posterior dorsal vertebrae. The best example is found in BP/1/ 6566, a posterior dorsal vertebrae where the right PIDF bears, at its deepest point, a sharp-rimmed oval pit reaching 11 mm in depth (Fig. 7B, D). The ostium of this subfossa is oval in shape, measuring 19 mm by 9 mm, with its long axis oriented dorsoventrally. It appears that the internal chamber of the subfossa expands beyond the medial lip of the ostium but this is difficult to determine because it has not been possible to clear the hard matrix from such a tight space. It also appears as though the compact periosteal bone surface of the vertebrae did not extend to the floor of the subfossa, thus leaving the internal trabecular bone exposed. Exposed trabecular bone within a pneumatic cavity is occasionally present in more derived sauropods; an example is shown in Martill and Naish (2001: 194, pl. 32).

The development of penetrative subfossae is sporadic within this taxon. The left side of the same vertebra displays a cluster of four small shallow dimple-like fossae that are separated by low rounded ridges in the same position as the well developed subfossa on the right side (Fig. 7C, E). A more posteriorly positioned neural arch (BP/1/ 6666, probably the 14th dorsal neural arch) lacks subfossae in its PIDF, whereas they are present in a dorsosacral neural arch (BP/1/ 5379: Fig. 8A). The latter specimen is incomplete, having

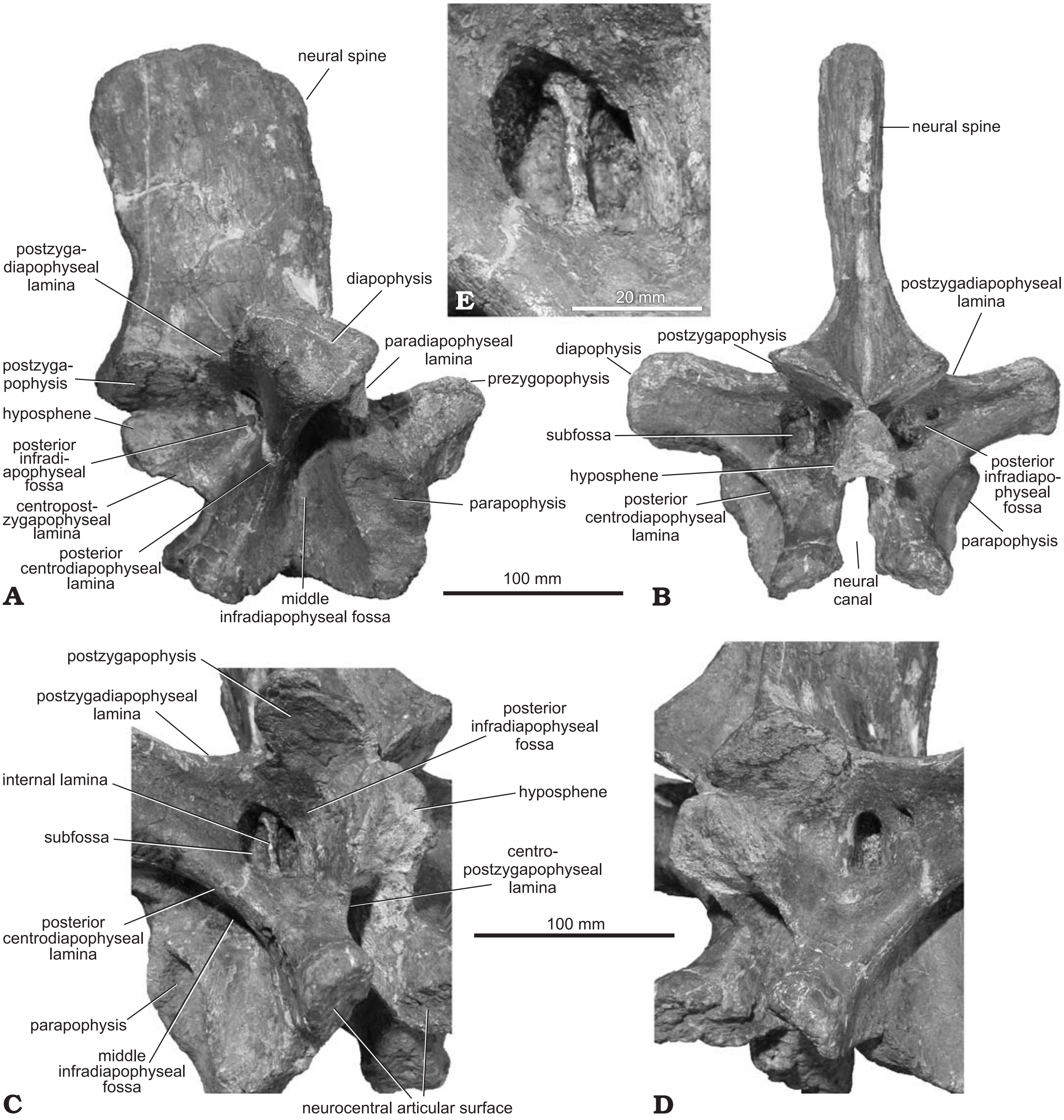

Fig. 9. Middle posterior dorsal vertebra of the basal sauropod *Antetonitrus ingenipes* Yates and Kitching, 2003, BP/1/4952 from the Upper Triassic Elliot Formation of Ladybrand, South Africa, in right lateral (**A**) and posterior (**B**) views. Left (**C**) and right (**D**) posterior infradiapophyseal fossa in oblique posterolateral and slightly ventral views. Close up of invasive left posterior infradiapophyseal subfossa (**E**).

been split coronally behind the enlarged sacral rib attachment and through the sacral homologue of the PIDF (Fig. 8A_1–A_3). Due to this damage it is not possible to provide measurements but it is clear that the subfossae are smaller than that of BP/1/ 6566 and have less distinct margins. Furthermore, these subfossae remain completely walled by compact bone. Nevertheless, they are in the same position at the deepest point of the infradiapophyseal fossa and are irregularly developed. The left side bears two such subfossae, arranged dorsoventrally with a low thick ridge separating the two whereas the right side has none. Interestingly the sacral centra of *Aardonyx* display laterally opening fossae behind

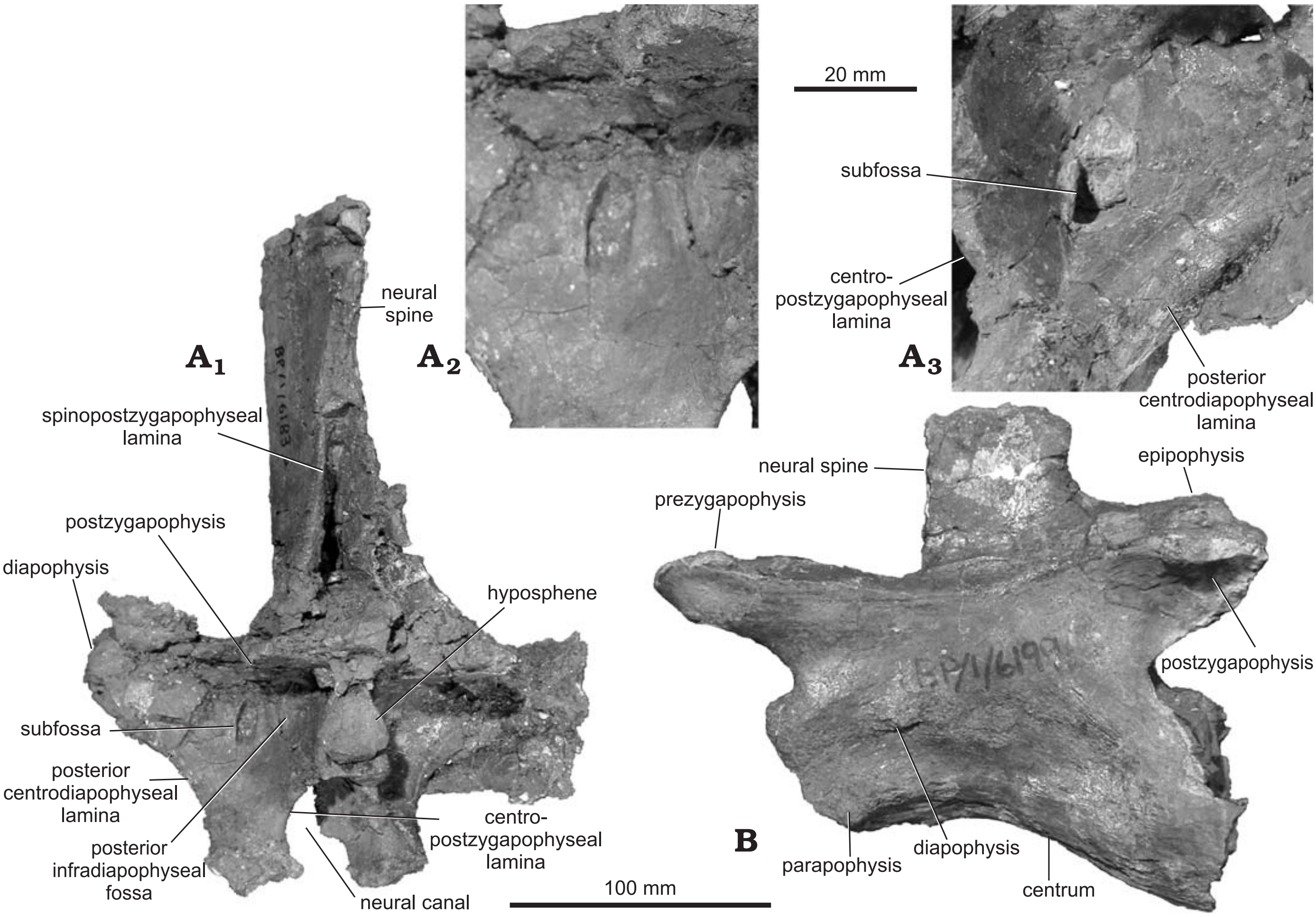

Fig. 10. Vertebrae of the Spion Kop sauropod from the Lower Jurassic Elliot Formation of South Africa. **A**. Posterior dorsal vertebra, BP/1/6183a in posterior view (A_1). Close-up of left (A_2) and right (A_3) posterior infradiapophyseal fossae. Note that the right subfossa cannot be seen in A_1 due to the oblique distortion of the specimen. **B**. Cervical vertebra, ?C3, BP/1/6199 in left lateral view.

the large attachment scars for the sacral ribs (Fig. 8B). Although quite deep, these pits differ from the infradiapophyseal subfossae in having smoothly rounded margins.

Antetonitrus (Fig. 9).—The mid-posterior dorsal neural arch of BP/1/4952 bears deep subfossae of likely pneumatic origin in the PIDF (Fig. 9). These are asymmetrically developed with a single large subcircular fossa developed on the left side and a narrower, arch shaped fossa on the right that is accompanied by two small ovoid accessory fossae. The large fossa on the left is 28 mm wide and 26 mm high. It reaches a depth of 23 mm. It is internally subdivided by a thin lamina that extends dorsoventrally. On the right side the large subfossa is 16 mm wide and 26 mm high. It is 22 mm deep, which is similar to the depth of the left subfossa. Given that the overall length of the neural arch from anterior to posterior most extension of the zygapophyses is 193 mm, the relative size of these fossae is substantial. The outer surface of compact bone forms a collar that extends for a short distance into the subfossae but it thins out leaving trabecular bone exposed in the deeper recesses of the subfossae. This bone is typical of non-pneumatised trabecular bone and is densely invested with tiny cancellous spaces, indicating that pneumatisation had proceeded no further than the subfossae. The exposed trabecular bone within the pneumatic cavity may indicate that pneumatic resorption was still occurring when the animal died. The small accessory subfossae on the right side are located laterally and ventrally to the main subfossa. They are ovoid shallow depressions of approximately 5 mm depth, and attaining a maximum diameter of 10 mm. The main subfossae are situated at the deepest point of the infradiapophyseal fossa. The MIDF is narrow and deep but does not bear distinct subfossae at its deepest point.

There are no subfossae in any of the infradiapophyseal fossae of a neural arch from near the posterior end of the presacral column (Yates and Kitching 2003: fig. 3d–f), nor are there any in the anterior dorsal neural arch (Yates and Kitching 2003: fig. 3a–c). The dorsal centra lack any obvious pneumatic features as does the sole cervical centrum.

Spion Kop sauropod (Fig. 10).—The cervical vertebra (BP/1/6199) is from a mature individual judging by the closure of the neurocentral sutures (Fig. 10B). Nevertheless it is a solid vertebra entirely lacking in pneumatic foramina or infradiapophyseal fossae. The middle dorsal neural arch (not figured) also lacks invasive pneumatic features although the AIDF, MIDF, and PIDF are present and well-developed. The posterior dorsal neural arch bears two subfossae, one in each PIDF (Fig. 10A). These subfossae are arch shaped, with parallel sides and a rounded dorsal margin as in the right subfossa of the *Antetonitrus* vertebra described above. They are about 15 mm high and 8 mm wide, with sharp medial, lateral and dorsal rims. The ventral margin forms a sloping ramp-like structure that suggests that the subfossa was created by a pneumatic diverticulum encroaching from the posteroventral direction. Poor preservation prohibits a determination of the depth of these structures. The anterior portion of this neural arch was destroyed by erosion, which has removed the MIDF and AIDF on both sides.

Discussion

Pneumatic origin of the subfossae.—There can be little doubt that the large subfossae that invade the neural arch from the wall of the PIDF in *Antetonitrus* are pneumatic in origin (Fig. 9C, D). Vertebral fossa-within-fossa structures are characteristic of pneumatised vertebrae (e.g., Wedel et al. 2000: figs. 7a, 8b) and are never, to our knowledge, caused by vasculature, fat bodies or muscles. Certainly the vertebral fossa of extant crocodilians that house fat and muscle do not feature fossa-within-fossa structures (O'Connor 2006: fig. 7). Secondly the subfossae of *Antetonitrus* are asymmetrically developed with the subfossa on the left side being internally subdivided by a lamina of bone. Asymmetrical subdivision of pneumatic fossae and chambers by internal laminae is typical in both birds and sauropods (e.g., O'Connor 2006: fig. 8d; Wedel et al. 2000: fig. 7a; Taylor and Naish 2007: figs. 3a, b, 4a, b). The fat and muscle bearing vertebral fossae of crocodilians do not display internal subdivision, asymmetrical or otherwise (O'Connor 2006: fig. 7). Lastly the depth of the subfossae would certainly count as invasive, even if the internal diameters of the chambers do not expand beyond the diameter of their external ostia.

The subfossae seen in the PIDF of the Spion Kop sauropod are also probably pneumatic in origin (Fig. 10A_2, A_3). The right subfossa of this sauropod has the same arch-like shape as the larger subfossa in the right infradiapophyseal fossa of *Antetonitrus* and the two structures would appear to be homologous. The subfossae of the Spion Kop sauropod are smaller than those of *Antetonitrus*. This may reflect a difference in the development of pneumatisation between the two taxa but it is more likely that the smaller vertebrae of the former are from an earlier stage of ontogenetic development.

Although most of the subfossae exhibited by *Aardonyx* are not as convincing, the oval subfossa developed in the PIDF of BP/1/6566 (Fig. 7D) is deep, blind ended, sharp rimmed and situated in exactly the same location as the definite pneumatic subfossae of *Antetonitrus* and the Spion Kop sauropod. Thus invasion by a pneumatic diverticulum is once again the most likely explanation for this feature. The identity of the deep fossae excavating the sacral centrum behind the attachment scars for the sacral ribs (Fig. 8B_3) is somewhat ambiguous due to their rounded margins and lack of internal expansion. Nonetheless the presence of similar fossae in the same position of sacral centrum 4 of the eusauropod *Haplocanthosaurus* (Wedel 2009: fig. 8a–d) does support the interpretation of the sacral fossa of *Aardonyx* as pneumatic. In both cases these fossae form conical pits excavated on the posterior dorsolateral surface, bounded anteriorly by the sacral rib attachment and posteriorly by the rim of the posterior face of the centrum. The fossae of *Haplocanthosaurus*, which are termed dorsolateral fossae by Wedel (2009) co-occur with typical lateral pneumatic fossae ("pleurocoels") in sacral centrum four, whereas they are absent in sacral centrum five which also lacks the lateral pneumatic fossae. This pattern of mutual occurrence and absence within the sacrum of *Haplocanthosaurus* strongly suggests that the sacral dorsolateral fossae are developmentally linked to the undoubtedly pneumatic lateral fossae. This, in turn, suggests that the dorsolateral fossae are themselves pneumatic in origin.

The internally subdivided pit excavated on the posterior cervical vertebra of AMNH 6810, *Plateosaurus* (Fig. 4B), is also considered to be the result of pneumatisation, as are the infradiapophyseal subfossae of SMNS F65. The location of the former on the anterior dorsolateral surface of the neural arch, near the base of the prezygapophysis differs from all the other pneumatic features described in this paper but is known site of invasion of diverticula from the cervical air sac system in extant birds (O'Connor 2006: fig. 2c). It is also internally subdivided by a lamina which further corroborates its identification as a pneumatic fossa.

The evolution of postcranial skeletal pneumaticity in Sauropodomorpha.—Armed with the knowledge that the structures observed in *Aardonyx*, *Antetonitrus* and the Spion Kop sauropod are likely pneumatic in origin, we can now turn our attention to the questions posed in the introduction. First and foremost the new observations indicate that invasive PSP evolved well before the origin of Eusauropoda rather than within that clade as has been previously supposed (e.g., Wilson and Sereno 1998; Wedel 2003b). Indeed its presence in *Aardonyx* indicates that invasive PSP actually precedes the origin of Sauropoda itself. Of course it may be argued that these are isolated autapomorphic occurrences and are not related to the development of the more extensive PSP seen in more derived eusauropods. However, all taxa from *Aardonyx* up to basal Gravisauria that have been adequately examined show the kind of PSP that is seen in the South African taxa. Parsimony would therefore suggest that this kind of PSP is a general character for basal sauropods and their closest relatives. Other, less well-exposed or less well-documented occurrences probably include the basal sauropod, or near-sauropod, *Camelotia* and the vulcanodontid *Tazoudasaurus*. *Camelotia borealis* is an incom-

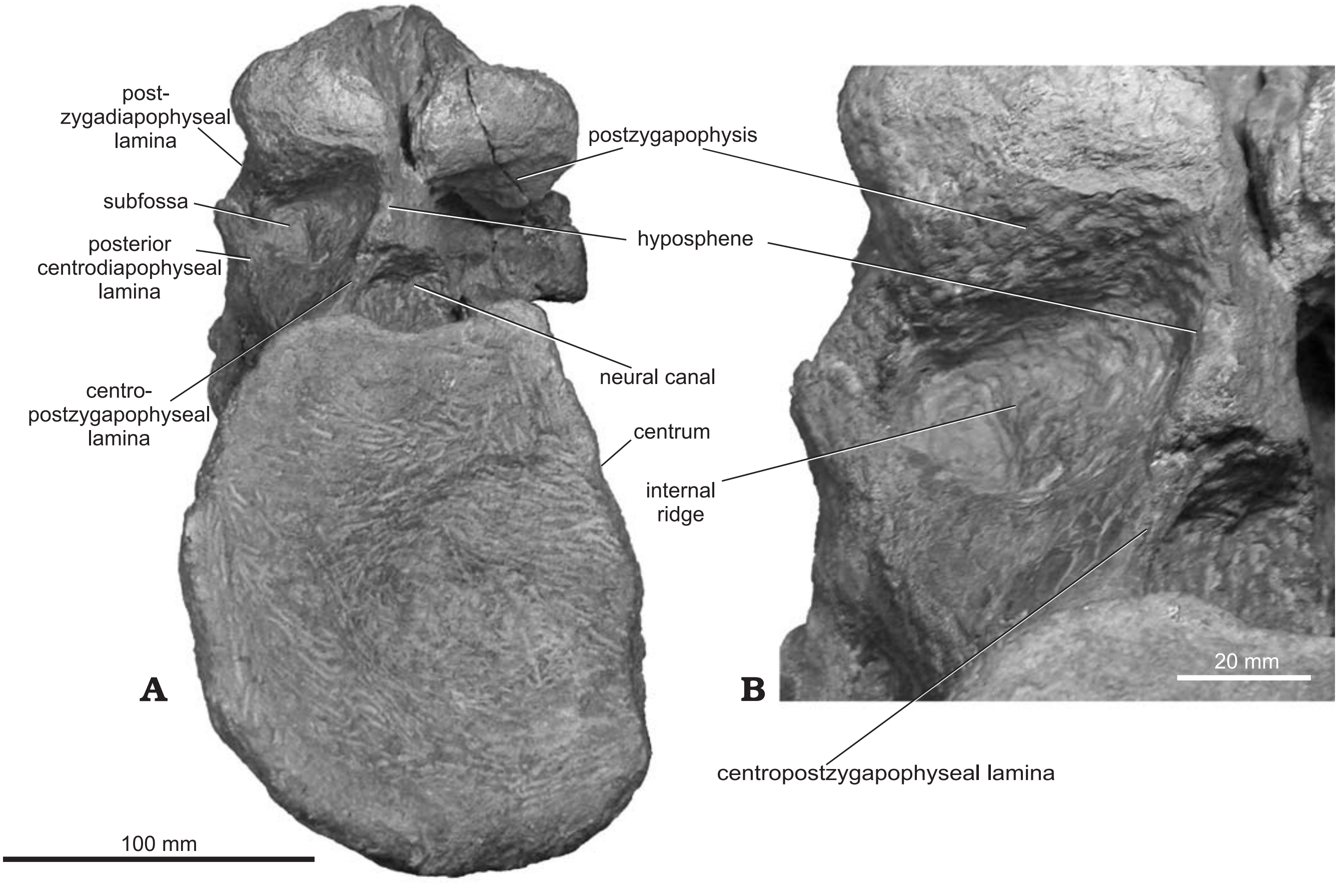

Fig. 11. Posterior dorsal vertebra of the basal sauropodomorph *Camelotia borealis* Galton, 1985, NHM R.2873 from the Upper Triassic Westbury Formation of Somerset, England. **A**. Posterior view. **B**. Close-up of left posterior infradiapophyseal fossa.

pletely known large early sauropodomorph whose affinities lie close to Sauropoda, if it is not actually a basal sauropod (Yates 2007). Its dorsal vertebrae are incompletely prepared with adherent matrix partially filling the infradiapophyseal fossae and obscuring the details of their walls. Nevertheless enough matrix has been removed from the left PIDF of NHM R.2873b, a large posterior dorsal vertebra, to reveal two subfossae separated by a ridge of bone (Fig. 11). However, it is not possible to determine the depth of the subfossae or the extent of the ostial rims due to the incomplete preparation.

The recent monographic description of the vulcanodontid *Tazoudasaurus naimi* also reveals features that appear to be the result of pneumatisation of the PIDF of posterior dorsal vertebrae (Allain and Aquesbi 2008). These appear as deep pits developed at the deepest point of the PIDF (Allain and Aquesbi 2008: fig. 14c, d). The cervical and anterior dorsal vertebrae of *Tazoudasaurus* possess deep fossae on the lateral surfaces of their centra like those of basal eusauropods. These structures have been shown to be the precursors of the more fully developed camerae and camellae present in derived eusauropods (Wedel 2003b). The middle dorsal vertebrae appear to lack both lateral fossae on their centra and subfossae within their infradiapophyseal fossae (Fig. 12). Thus *Tazoudasaurus* may be an example of a pneumatic hiatus (Wedel 2003a, 2009). However, we argue below that the infradiapophyseal fossae of all saurischians are pneumatic features so it might be better to term this gap as a pneumatic attenuation rather than a full hiatus. Nevertheless the PSP is more invasive on either side of the attenuated zone and this suggests that the vertebrae of this taxon were pneumatised by diverticula from different sources. O’Connor and Claessens (2005) found a similar pattern of pneumatisation in the abelisaurid theropod *Majunasaurus*, and suggested that PSP tends to attenuate as pneumatic diverticula get farther from the lungs and air sacs that produce them.

There are no basal sauropods or near-sauropods that positively lack pneumatic foramina in the PIDF of the posterior dorsals. Apart from those described in this paper, all other non-gravisaurian sauropods and advanced anchisaurs (e.g., *Melanorosaurus*) lack sufficiently well preserved and/or described dorsal vertebrae to make a determination. Thus, given the evidence at hand, it is most parsimonious to assume that the presence of infradiapophyseal PSP is the basal condition for Sauropoda. It is important to note that without very well prepared specimens (or CT scans) these features are easily overlooked. The large well developed chambers of *Antetonitrus* lay hidden behind a cover of matrix and glue in a specimen that otherwise appeared to be well-prepared.

It appears that the evolution of sauropodomorph PSP proceeded in a very different manner to that of theropods. The

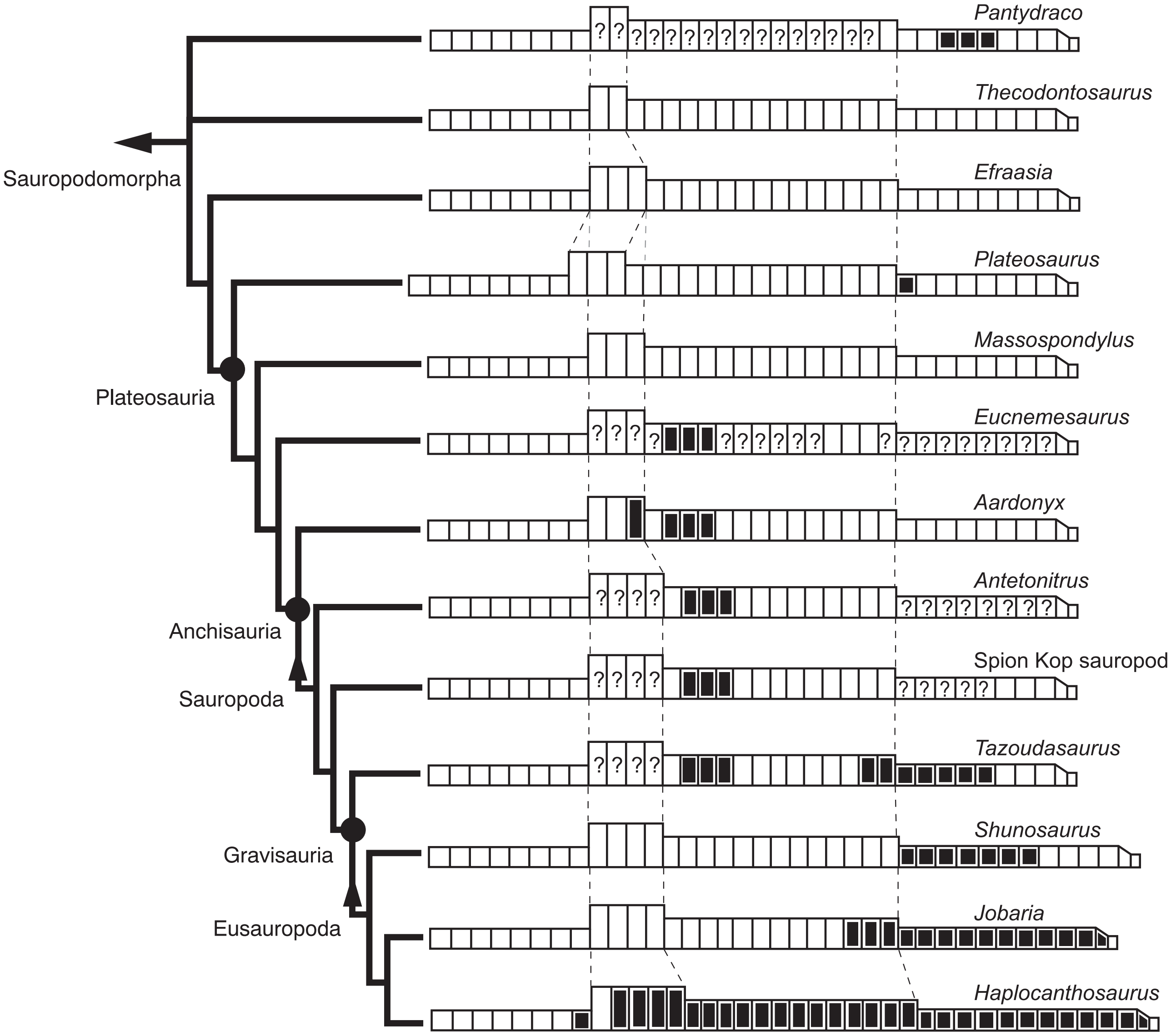

Fig. 12. A phylogenetic diagram showing the distribution of invasive PSP along the vertebral column (the caudal series is truncated) in Sauropodomorpha. Black boxes indicate the presence of pneumatic fossae or invasive infradiapophyseal subfossae. Note that in the case of *Plateosaurus* PSP is presently known in a single specimen whereas other specimens of same taxon lack it. The phylogeny is based on Yates (2010), with the modification that *Eucnemesaurus* is placed closer to Anchisauria than *Massospondylus* is. The position of the Spion Kop sauropod is based on an unpublished analysis (AMY unpublished data). The distributions of PSP in the taxa not directly examined in this study were gleaned from the following sources: *Pantydraco* (Yates 2003; Wedel 2007), *Tazoudasaurus* (Allain and Aquesbi 2008), *Shunosaurus* (Zhang 1988), *Jobaria* (Sereno et al. 1999), *Haplocanthosaurus* (Hatcher 1903).

basal most occurrence of invasive PSP in Theropoda occurs in the recently described *Eodromaeus*, where there are pneumatic fossae developed on the sides of the mid-cervical centra (Martinez et al. 2011). In Coelophysoidea, the basal most neotheropods, the extent of pneumatisation has expanded so that pneumatic fossae occur in the postaxial cervical centra and the anteriormost dorsals (Rowe and Gauthier 1990; Rauhut 2003). PSP is variable in derived theropods but numerous taxa evolved more extensive PSP that extends forward into the axis and back into the rest of the dorsal column, and in some cases the sacrum and proximal caudal vertebrae (e.g., *Majungasaurus*, O'Connor and Claessens 2005; O'Connor 2007; *Acrocanthosaurus*, Harris 1998; *Aerosteon*, Sereno et al. 2008; *Tyrannosaurus*, Brochu 2003; *Nomingia*, Barsbold et al. 2000). A similar pattern is seen in modern avian ontogeny where pneumatic diverticula from the cervical air sac system in the midcervical region are the first to form PSP (Cover 1953; Hogg 1984; Bezuidenhout et al. 1999). Initially it was thought that Sauropodomorpha might follow a similar pattern based on the early appearance of weakly developed pneumatic features in the midcervical vertebrae of the basal sauropodomorph *Pantydraco caducus* and the posterior progression of pneumatic vertebrae in eusauropod phylogeny (Wedel 2003b, 2007). Nevertheless the pneumatic features of *Pantydraco* appear to be phylogenetically isolated and most other non-anchisaurian sauropodomorphs have apneumatic cervical vertebrae (Fig. 11), with the exception of some individuals of *Plateosaurus*. The features of the South African taxa described here indicate that PSP actually begins near the posterior end of the presacral column in advanced anchisaurian sauropodomorphs and is inherited by the earliest sauropods. Only later, toward the end of the Early Jurassic, do gravisaurs develop PSP of the cervical vertebrae that then progresses posteriorly (Fig. 12). Our current knowledge would suggest that the initial posterior PSP of the infradiapophyseal fossae was lost soon after this time, only to be reacquired in some derived neosauropods such as *Apatosaurus*; (Wedel 2007: fig. 3c) and *Erketu* (Ksepka and Norell 2006: fig. 7d). Janensch (1947) also noted that the infradiapophyseal fossae of most eusauropods were devoid of pneumatic foramina despite their development at this position in several theropods, including extant birds. He suggested that the thin lamellar construction of derived eusauropod neural arches may well prevent the development of infradiapophyseal pneumaticity by simply not providing enough internal volume for the pneumatic diverticula to invade. This explanation works well for derived eusauropods but does not explain the apparent absence of infradiapophyseal pneumatic fossae in basal eusauropods such as *Shunosaurus* which have relatively solid neural arches. Nevertheless, we must caution that the pneumatic fossae of the infradiapophyseal fossae are not large or obvious and they may have simply been overlooked in basal eusauropods. The re-acquisition of infradiapophyseal pneumaticity in some derived neosauropods may be a result of the development of camellae in the neural arches which “inflate” their volume, and thus make invasion by external pneumatic diverticula viable once again.

Abdominal air sacs in non-avian dinosaurs.—Extant birds primitively possess nine air sacs, although this number is reduced in several clades by loss or fusion: a single clavicular sac, and paired cervical, anterior thoracic, posterior thoracic and abdominal air sacs (McLelland 1989). However, only the cervical air sacs, abdominal air sacs and lungs produce pneumatic diverticula that invade the vertebral column (O’Connor and Claessens 2005). There has been confusion concerning which air sac systems were responsible for the PSP seen in non-avian dinosaurs. Extant birds show an unambiguous pattern of site-specific invasion (O’Connor and Claessens 2005; O’Connor 2006). The cervical air sac system pneumatises the cervical vertebrae and the anterior dorsal vertebrae up to the level of the lungs but no further (O’Connor and Claessens 2005). The abdominal air sacs pneumatise the dorsal vertebral column posterior to the lungs and the synsacrum (as well as some bones of the pelvic girdle and hindlimb). Thus the presence of PSP in the posterior dorsal, sacral and caudal vertebrae of derived eusauropods is good evidence for the presence of abdominal air sacs in these dinosaurs. O’Connor and Claessens (2005) have used the same argument to infer the presence of abdominal air sacs invading the posterior dorsal column and sacrum of derived neotheropods (Ceratosauria + Tetanurae) and backed it up with a comprehensive survey of PSP in extant avians. Nevertheless Sereno et al. (2008) recently resurrected the hypothesis that the cervical air sac system was responsible for pneumatisation of the entire presacral column in non-avian dinosaurs. Sereno et al. (2008) supported their case with two lines of evidence. Firstly they cite anatomical work that had found the pneumatic diverticula of the cervical air sac system that extend posterior to the lungs in ostriches (McLelland 1989; Bezuidenhout et al. 1999). Secondly they observed that the pneumatic features of the presacral column in non-avian dinosaurs are remarkably uniform, suggesting a single anatomical source. A closer look at the papers investigating the pneumaticity of ostriches reveals that although there are posterior pneumatic diverticula of the cervical air sac system these are lodged in the peritoneal cavity and are remote from the posterior dorsal vertebrae which are pneumatised by the abdominal air sacs as in all other birds (McLelland 1989; Bezuidenhout et al. 1999). The second point is uninformative

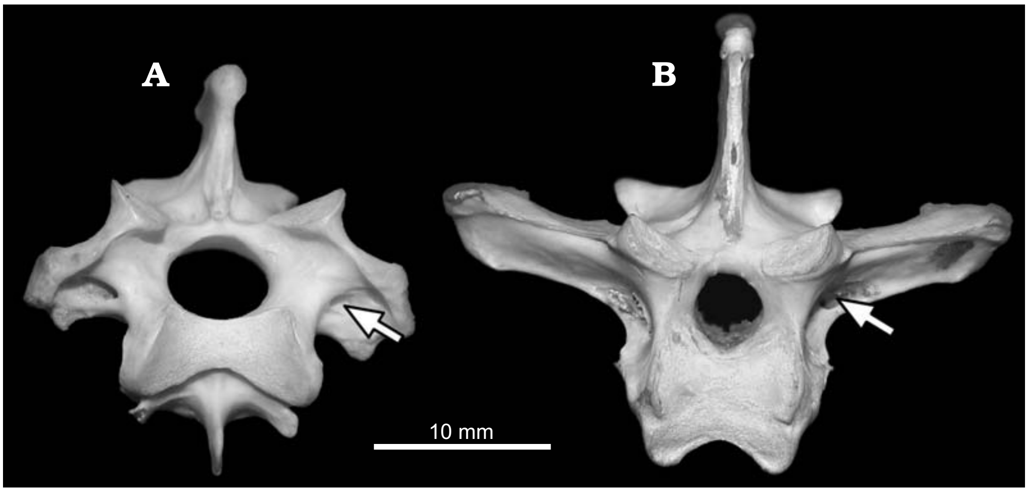

Fig. 13. Vertebrae of the helmeted guinea fowl, *Numida meleagris* (Linnaeus, 1758), BP/4/1332 from Gauteng, South Africa, in anterior view. **A**. Last free cervical, C15. **B**. Last presacral thoracic, T4. Arrows point to the main pneumatic foramina of each vertebra. Note that the pneumatic foramina occur on the anteroventral surface of the transverse processes of both vertebrae despite being formed by diverticula from different sources. In A the diverticula extend from the cervical air sac system whereas in B the foramina result from the activity of diverticula from the abdominal air sacs.

because modern birds also possess uniform pneumatic features along their presacral column despite being created by pneumatic diverticula from three different sources: the cervical air sacs, the lungs and the abdominal air sacs (Fig. 13).

Thus in extant birds the presence of PSP in the posterior dorsal column is diagnostic of the presence of abdominal air sacs. However, modern birds are but one surviving clade of saurischian dinosaurs. One could imagine a scenario in which initial pneumatisation along the presacral column was created by diverticula from the cervical air sac system with the diverticula of the abdominal system only displacing the cervical system in the posterior dorsals at a later date, when the abdominal system had evolved (Sereno et al. 2008). This scenario is less parsimonious, since it relies on a developmental pattern that has never been observed in extant animals, and it is potentially falsified by the presence of something very like a posterior dorsal pneumatic hiatus (that is, "a gap in pneumatisation between diverticula of the cervical air sacs or lungs and diverticula of the abdominal air sacs"; Wedel 2009: 618) in *Tazoudasaurus*.

Our findings help to resolve this issue in favour of the presence of abdominal air sacs in sauropodomorph dinosaurs (and by use of the phylogenetic bracket, non-avian theropods as well). The region of pneumatisation in both *Aardonyx* and the Spion Kop sauropod is the middle posterior region of the dorsal column. In both cases the anterior dorsal and cervical vertebrae are known to lack specific pneumatic features (other than the infradiapophyseal fossae). In extant birds post-cervical pneumatisation begins adjacent to the lungs or the air sacs themselves and spreads further afield as ontogeny progresses. In other words, the South African sauropodomorphs show invasive pneumatisation in the region known to be pneumatised by diverticula from abdominal air sacs and only in that region. For this pneumatisation to have been caused by diverticula from the cervical airsac system not only would the cervical diverticula have had to have spread further posterior than in any extant bird, but they also would have to have passed over the cervical, anterior dorsal and middle dorsal vertebrae before beginning to invade the posterior dorsal vertebrae. This is a decidedly unparsimonious, convoluted and unnecessary scenario. Thus we can confidently infer that diverticula from the abdominal air sacs were responsible for the pneumatic features of basal sauropods and advanced anchisaurs.

The presence of abdominal air sacs has important biological implications. Unlike the cervical air sac system the abdominal system is a compliant ventilatory system that is used by extant birds to provide flow-through ventilation to rigid, non-compliant, parabronchial lungs (Duncker 1971). These lungs are highly efficient gas-exchangers and allow birds to maintain high rates of oxygen consumption associated with sustained aerobic exercise (Scheid 1979). Recent work has shown that crocodilians also utilise one-way, flow-through ventilation (Farmer and Sanders 2010), which strongly suggests that this form of ventilation is the basal condition for Archosauria and preceded the evolution of air sacs and rigid lungs. The latter would then represent a further elaboration of respiratory style inherited from the archosaurian common ancestor. It is also probable, though difficult to test at present, that compliant ventilatory air sacs, such as abdominal air sacs, and rigid, parabronchial lungs are two parts of one system that evolved hand-in-hand and that neither ever existed without the other.

We propose that a full complement of air sac systems coupled with flow-through ventilation of rigid parabronchial lungs was present in the sauropodomorph lineage before any of these air sacs began to invade the postcranial skeleton. The sporadic occurrence of pneumatic features in basal sauropodomorphs (e.g., *Pantydraco* and *Plateosaurus*) is easy to understand if the evolution of air sac diverticula preceded the evolution of PSP: they represent independent, small-scale acquisitions of the ability for pneumatic diverticula to invade bone.

From this it would seem likely that pneumatised neornitheans and advanced sauropodomorphs inherited their compliant air sac system from the eusaurischian common ancestor, which in turn may have inherited it from an earlier ancestor possibly extending back to predinosaurian dinosauriforms. The presence of PSP in pterosaurs, including basal forms (Butler et al. 2009a), raises the possibility that this system evolved soon after Avemetatarsalia ("bird-line" archosaurs) split from the Pseudosuchia ("crocodile-line" archosaurs).

The early evolution of air sacs.—To better address the question of when these air sac systems evolved, we need to recognise earlier stages of pneumatisation that do not display the classic morphology of expanding internal chambers that communicate with the exterior of the bone via sharp-rimmed foramina. The posterior dorsal vertebra of *Eucnemesaurus*, a "prosauropod-grade" sauropodomorph possibly related to *Riojasaurus* is significant in this regard. As in *Aardonyx* and *Antetonitrus*, it possesses subfossae in the PIDF (Fig. 5). However, these are shallow depressions that lack sharp margins. By themselves they constitute poor evidence for the presence of pneumatic diverticula. Nevertheless, these depressions are developed in exactly the same position as the diagnostic pneumatic foramina of *Antetonitrus*, that is, at the deepest point of the PIDF of the posterior dorsal vertebrae. It is important to note that pneumatisation of the cervical air sac system in both theropods and sauropods begins with shallow fossae with rounded rims that are nonetheless developed at the same place that later develop incontrovertible pneumatic features (Wedel 2003a, 2007: fig. 9). From this we conclude that the subfossae of *Eucnemesaurus* were probably created by pneumatic diverticula that were housed in the infradiapophyseal fossae.

Lastly, we can explore more speculative ideas on the origin of pneumatic diverticula. If we accept that the infradiapophyseal fossae of basal sauropodomorphs housed pneumatic diverticula then it seems extremely likely that the common ancestor of Eusaurischia did so as well, given that both Theropoda and Sauropodomorpha possess such infradiapophyseal fossae and both lineages eventually produced PSP. Further supporting evidence that the infradiapophyseal fossae of basal sauropodomorphs housed pneumatic diverticula can be gleaned from their anatomical distribution. Infradiapophyseal fossae extend from the cervical series to the sacrum where they end abruptly. A point of terminology needs to be cleared up here: despite the name, infradiapophyseal fossae occur between laminae that extend from the transverse processes of vertebrae, regardless of whether or not a diapophysis is present at its distal end. Proximal caudal vertebrae of basal sauropodomorphs lack infradiapophyseal fossae despite having large transverse processes with fused caudal ribs. This casts doubt on the hypothesis that the diapophyseal laminae that bound the infradiapophyseal fossae are a structural consequence of vertebral construction and is concordant with the hypothesis that infradiapophyseal fossae housed pneumatic diverticula. Further support can be garnered from the mutual distribution of diagnostic pneumatic foramina and infradiapophyseal laminae in the proximal caudal vertebrae of neosauropods. In some lineages, such as diplodocids and titanosaurs, PSP extends posteriorly into the base of the tail and so too do the infradiapophseal laminae and their attendant fossae (e.g., Wilson 1999: fig. 4). These mutual co-occurrences suggest that the two features are linked, probably because they are both reflections of the presence of pneumatic diverticula.

Eusaurischians inherited their well-developed infradiapophyseal fossae from earlier dinosauriforms. Non-dinosaurian dinosauriforms such as *Silesaurus* have infradiapophyseal fossa as well developed as those of any basal sauropodomorph (Dzik 2003). Might these have housed pneumatic diverticula as well? Most researchers have cautiously stepped away from reaching such a conclusion because simple fossae are known to house other soft tissues in modern vertebrates. Nonetheless, Butler et al. (2009a) speculate that the exceptional depth of these fossae, the thinness of the intervening laminae and the presence of laminae that are otherwise unique to Saurischia are suggestive of a pneumatic origin. We note that these structures are phylogenetically continuous with those of basal sauropodomorphs and there is no indication that some other soft tissue was switched with pneumatic diverticula at any point in the continuum between nondinosaurs like *Silesaurus* and incontrovertibly pneumatised saurischians. In the absence of evidence for such switching it is most parsimonious to assume that the infradiapophyseal fossae of saurischian dinosaurs and their dinosauriform forebears were receptacles for pneumatic diverticula from their inception. Note that this argument rests heavily on phylogenetic distribution and we are not suggesting that phylogenetically disjunct occurrences of infradiapophyseal fossae, such as have been reported in *Erythrosuchus* (Gower 2001), poposauroids (Nesbitt 2005, 2007; Butler et al. 2009b) and various crocodyliforms (e.g., Wedel 2007), necessarily record the presence of pneumatic diverticula, although they might. Indeed the development of a *Eucnemesaurus*-like subfossa within the PIDF of the possible ctenosauriscid poposauroid *Hypselorhachis* (Butler et al. 2009b: fig. 2h) is especially intriguing in this regard.

Our hypothesis also requires that the capacity for pneumatic invasion of the postcranial skeleton was lost in the ornithischian lineage; however, this capacity has also been lost in several lineages of birds including terrestrial forms (e.g., *Apteryx*, Owen 1839), so it is not an insurmountable difficulty. It may pay to examine ornithischian fossils more closely for subtle, poorly-developed pneumatic features such as those described in this paper. We suggest that a fully avian style air-sac system, complete with compliant, ventilatory air sacs was an ancient feature that had evolved prior to the initial radiation of the dinosaurs and indeed may have facilitated that radiation.

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