

A NEW CRUROTARSAN ARCHOSAUR FROM THE LATE TRIASSIC OF SOUTH WALES

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ABSTRACT—We report a third archosaur from the Late Triassic cavity-fill sediments of Pant-y-ffynnon Quarry in South Wales, in addition to the basal crocodylomorph *Terrestrisuchus* and the basal sauropodomorph dinosaur *Pantydraco*. The new taxon, *Aenigmaspina pantyffynnonensis*, previously referred to informally as ‘Edgar,’ was recovered in 1952 and is preserved as a tight cluster of vertebrae, ribs, and a scapula in a single block, as well as numerous associated, but now isolated, elements, including skull bones, vertebrae, further putative elements of the forelimb, and a partial pelvis. We present a digital model based on computed tomography (CT) scans of the main associated blocks, which shows exquisite detail of an associated series of 12 cervical and anterior dorsal vertebrae, with ribs and a scapula. The well-developed spine tables and eight matching osteoderms confirm that this is a crurotarsan archosaur, but it lacks apomorphies of all major crurotarsan clades. Phylogenetic analysis gives equivocal results, showing weak relationships with Proterochampsidae and Ornithosuchidae; the new taxon might lie close to Erpetosuchidae, based on the ‘Y’-shaped spine tables.

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INTRODUCTION

The Late Triassic was a time of great change in tetrapod faunas, as archosaurs rose to ever greater ecological prominence and dinosaurs took over the world. The Triassic rise of the dinosaurs was a three-step process: the first step being the origin of Dinosauria in the Early Triassic in the aftermath of the Permian–Triassic mass extinction, then their expansion in ecological dominance following the Carnian Pluvial Event, 232 Ma, and finally a substantial diversification after the end-Triassic mass extinction (Langer et al., 2010; Benton et al., 2014; Bernardi et al., 2018). At the same time as the diversification of the dinosaurs, pterosaurs, and their close relatives (the Avemetatarsalia or ‘bird-line archosaurs’), including the basal Aphanosauria (Nesbitt et al., 2017), the other major branch of Archosauria, the Crurotarsi or ‘crocodile-line archosaurs,’ were also making an ecological impact. Whereas much attention focuses on the larger archosaurs of the Late Triassic, small archosaurs, as well as sphenodontians, mammals, and tritylodonts, are sampled by certain unusual sedimentary deposits worldwide. Classic examples are the Bristol-South Wales fissures, a suite of cavity fills of Late Triassic to Early Jurassic age that are well known from a dozen Carboniferous limestone quarries (Whiteside et al., 2016).

Late Triassic crurotarsans include phytosaurs, aetosaurs, ‘rauisuchians,’ ornithosuchids, gracilisuchids, erpetosuchids, and crocodylomorphs (e.g., Brusatte et al., 2010; Nesbitt, 2011; Ezcurra et al., 2017). Phytosaurs were semiaquatic organisms with a long snout

and some dermal armor, giving them a superficial resemblance to modern fish-eating gharials. Aetosaurs were heavily built quadrupeds, mostly with blunt snouts and teeth adapted for herbivory, and with extensive dermal armor; these osteoderms are in many cases their most defining feature and the most common fossil remains of the group (Scheyer et al., 2014). ‘Rauisuchians’ are a paraphyletic group comprising some very large quadrupeds and bipeds, important in most ecosystems as top carnivores. Ornithosuchids are a small group of carnivores, some bipedal. There were also other smaller clades of Late Triassic crurotarsans, including gracilisuchids and erpetosuchids, mainly small in size. Finally, the crocodylomorphs of the Late Triassic include small bipedal forms but were still mainly terrestrial. Phytosaurs, aetosaurs, ‘rauisuchians,’ and ornithosuchids all went extinct during the end-Triassic mass extinction, and only the crocodylomorphs survived, diversifying in the Jurassic as freshwater, terrestrial, and marine forms (Brusatte et al., 2010; Nesbitt et al., 2013, 2017; Butler et al., 2014; Ezcurra et al., 2017).

The subject of this paper is a small crurotarsan archosaur from a Late Triassic fissure in Pant-y-ffynnon Quarry, South Wales, United Kingdom. Fossil vertebrates were first reported from Pant-y-ffynnon by Kermack (1956), and his collections formed the basis for the subsequent description of three new species: the crocodylomorph *Terrestrisuchus gracilis* (Crush, 1984), the sauropodomorph dinosaur *Pantydraco caducus* (Kermack, 1984; Galton and Kermack, 2010), and the sphenodontian *Clevosaurus cambrica* (Keeble et al., 2018). Other fossils include two additional sphenodontians: *Diphydontosaurus* and an unnamed form, as well as a coelophysoid theropod (Rauhut and Hungerbühler, 2000). A kuehneosaur was noted earlier (Crush, 1984; Galton and Kermack, 2010), although we (Keeble et al., 2018) could not confirm this. Previous accounts of the Pant-y-ffynnon vertebrate fauna have referred to an additional taxon, a crurotarsan archosaur informally named ‘Edgar’ by Kermack and his

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team (Kermack, 1956; Fraser, 1994; Galton and Kermack, 2010; Keeble et al., 2018), and the aim of this paper is to present Edgar to the world and interpret its phylogenetic position and place in the ecosystem.

Institutional Abbreviation—NHMUK, Natural History Museum, London, U.K.

GEOLOGICAL SETTING

The specimen comes from Pant-y-ffynnon Quarry (Fig. 1), which is a well-known source of diverse fossil reptiles (Keeble et al., 2018). For full details of the quarry and location, see Keeble et al. (2018). The site has long been quarried for the Lower Carboniferous limestones that make up the bulk of the rock in the quarry, but occasionally the quarrymen hit fissures filled with a range of gray, brown, buff, or yellow-colored sediment; it was these fissure fills that contained the bones. There are in fact two quarries at Pant-y-ffynnon, a northern and a southern quarry (U.K. grid references ST 046 742 and ST 046 740, respectively) on either side of an unclassified road. The smaller northern quarry is the older, and it is the only one shown on Ordnance Survey maps from the 1910s to the 1960s. The notes of Kenneth Kermack (1919–2000) and Pamela L. Robinson (1919–1994) confirm that they visited both quarries regularly but recovered vertebrates only from the northern quarry (Keeble et al., 2018). Kermack documented the growing work at the new southern quarry, initially at a slow speed before expanding to yield, each year, an estimated 100,000 tons of Carboniferous limestone. The University College London (UCL) team appears to have collected specimens in Pant-y-ffynnon Quarry only from spoil heaps left by the quarrymen, and it is uncertain whether the spoil came from one or several fossiliferous fissures. However, Kermack et al. (1973:table 2) mentioned only one fissure system in Pant-y-ffynnon.

The Bristol-South Wales fissures (Fig. 1) span an age range from Late Triassic to Early Jurassic, and it has proved difficult to assign ages with confidence to all of them (Whiteside et al., 2016). There are two broad fissure types: those containing sediments with reptiles, dated to the Late Triassic, and those containing sediments with mammals, reptiles, and tritylodonts, dated to

the Early Jurassic (Robinson, 1957; Whiteside et al., 2016). The Pant-y-ffynnon tetrapod fauna indicates a Triassic age, and the green and yellow (ochreous) colors of the sediments confirm this. In earlier reports, the age was suggested to be Carnian or Norian (Shubin and Sues, 1991; Benton, 1994; Benton and Spencer, 1995), based on the supposedly primitive nature of many of the reptile fossils. Robinson (1971) and Crush (1984) suggested that the Pant-y-ffynnon fissure deposits were Norian, whereas Warrener (1983), quoted in Evans and Kermack (1994), suggested that they were ‘Rhaeto-Liassic,’ and possibly Hettangian. The Pant-y-ffynnon reptilian fauna is most like that from Tytherington Quarry; the Tytherington fissure tetrapods are associated with palynomorphs that indicate an early Rhaetian age (Whiteside and Marshall, 2008; Whiteside et al., 2016), and this has been accepted by others (Galton and Kermack, 2010; Keeble et al., 2018). Additional age evidence was presented by Morton et al. (2017), who identified conchostracans from Cromhall that dated some fissure infills there as late Rhaetian in age (equivalent to the Cotham Member, Lilstock Formation), and they reported a solitary conchostracan, *Euestheria* cf. *brodieana*, from a Pant-y-ffynnon fissure deposit (Morton et al., 2017: fig. 12g) with the same lithology as the tetrapods, perhaps indicating a similar age.

The Edgar specimen was collected in 1951 or 1952 by Kenneth A. Kermack and Pamela L. Robinson during one of several visits around that time to the site (Kermack, 1956). That short note reported an abstract of a talk delivered on October 8, 1953, during which Kermack (1956:1) said, “During an extensive survey of fissures occurring in the Carboniferous Limestone of Glamorgan, carried out by Miss Robinson and myself in the Spring of 1952, a bone-bearing locality, probably of Late Triassic age, was discovered at Pant-y-ffynnon [sic] quarry, near Cowbridge. The bones are in an excellent state of preservation, and comprise five species of reptiles.” That, and information from notes left by Robinson, indicates that the collection was made during that one trip. The investigators noted that there were rather complete skeletons, representing five species, of which three have now been described and named, the crocodylomorph *Terrestrisuchus gracilis*, the sauropodomorph dinosaur *Pantyracosaurus caducus*, and the sphenodontian *Clevosaurus cambrica*.

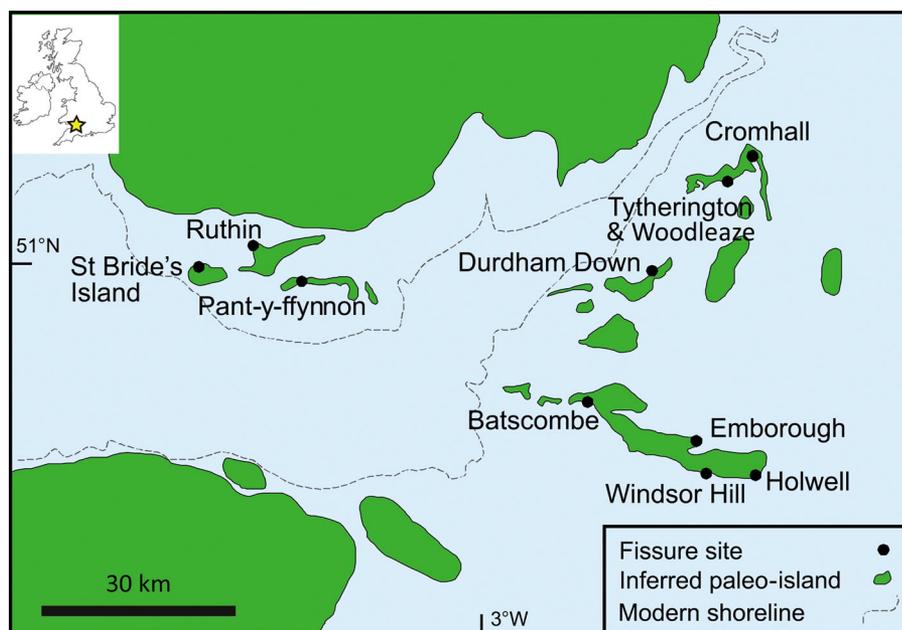


FIGURE 1. Map of the Late Triassic and Early Jurassic fissure localities of southwestern United Kingdom, with land masses and reconstructed paleo-islands indicated in green. Modified from Keeble et al. (2018).

The fourth is Edgar, and the fifth species was the ‘coelophysoid’ dinosaur noted by Warrener (1983) and described by Rauhut and Hungerbühler (2000) as similar to ‘*Syntarsus*’ (= *Coelophysis*), but which Keeble et al. (2018) could not locate. Blocks of fossiliferous matrix from Pant-y-ffynnon that were processed by Keeble et al. (2018) bore the date 1951 (a date also given on an envelope with notes on the collection made by Robinson), so it is unclear whether Kermack and Robinson had visited the quarry earlier and collected these blocks before their 1952 visit, or whether Kermack (1956) was in error in stating that the Kermack-Robinson survey had been done in 1952. Kermack’s notes show that he and his UCL team regularly revisited the quarries from 1952 to 1982, but they found nothing after 1952, it seems (Keeble et al., 2018).

The fact that the Pant-y-ffynnon reptiles are so well articulated and complete is most unusual because most other fissure deposits in South Wales and around Bristol yield isolated tetrapod fossils that have been transported and disarticulated (Robinson, 1957; Whiteside et al., 2016). The Pant-y-ffynnon vertebrate fossils all came from spoil heaps, and Kermack and colleagues tried to keep the material associated. In most cases, there was a single block containing the bulk of the skeleton, plus other pieces from nearby that could be fitted to the main block. As with previous descriptions of these other taxa (e.g., Warrener, 1983; Crush, 1984; Galton and Kermack, 2010; Keeble, et al., 2018), we assume that the fact the remains were collected as an associated set means that they were likely multiple parts of the skeleton of a single individual of a particular species. Nonetheless, we test the plausibility of association of all loose pieces that cannot be fitted directly to the main blocks in terms of whether they could be assigned to any other taxa known from the site or to the present taxon, based on apomorphic characters, general resemblance, and size comparison.

The bones from the different fissure deposits vary in color, and the colors reflect the original oxidation conditions of the depositional environment (Whiteside et al., 2016). The Pant-y-ffynnon bones described here are white, indicating that they came from oxygenated settings.

MATERIALS AND METHODS

We have examined 44 specimens donated by Pamela Robinson and Kenneth Kermack to the NHMUK that, based on Robinson’s notes (held by NHMUK), were found at the same time. These cannot be guaranteed to be from the same individual and may have been simply found near each other. Further, since their discovery, the specimens have been extensively prepared to remove the sediment from the tiny bones, but we have not located any preparation records. The preparation, however, sometimes included removing bones completely from their host blocks, and now we can only use the informal numbers (Appendix 1) as the sole clue to any possible associations.

Two bone-packed, prepared blocks bearing the number P9/3a fit together (Fig. 2), and these (right scapula, 12 cervical and dorsal vertebrae in sequence, ribs, osteoderms) are the focus of our study. We assumed that the other three separately packed specimens numbered P9/3a (left distal scapula, left humerus, vertebra) had been removed from these blocks during preparation; these three all bear additional labels that state ‘No. 11.’ Two further specimens, numbered P9/1a and P9/2a (distal end of a humerus and a proximal end of a right humerus), might also be associated. So far, there are no implausible components in terms of duplicates or specimens of inappropriate size or morphological attribution.

The remaining 37 specimens bear different kinds of informal numbers, ranging from P26/1 to P141/1A (Appendix 1), and, without further information, it is impossible to know what they mean. In fact, these numbers are entirely overlapped by the

numbering scheme for specimens of *Terrestrisuchus* (Crush, 1984), ranging from P47/21 to P130/1, and *Pantydraco* (Galton and Kermack, 2010), ranging from P6/1 to P141/1. Therefore, there is a risk that we are looking at a series of specimens that were not claimed by the describers of those two taxa, and so these leftovers might pertain to many taxa. However, they are of plausible size to belong to the core material of the new archosaur and are elements of small, slender-limbed archosaurs. However, there are duplicate elements, for example, two left humeri (P50/4, P141/1A) and two right scapulae (P9/3a, P49/1). Therefore, we present these additional materials cautiously and in sequence of likelihood of attribution to the same animal, using evidence from the informal numbering and labeling first, then general size, lithology, and phylogenetically plausible anatomical characters.

Photographs were taken with fixed lights in a darkened room using a Nikon digital single-lens reflex camera. In addition, the two pieces numbered P9/3a and P49/1 were three-dimensionally imaged using the Nikon XT H, 225 ST CT scanner in the Palaeobiology Research Group at the University of Bristol. The P9/3a specimens were segmented using the Avizo 9.4 Lite software package, but P49/1 did not produce results of usable quality and was abandoned. The automatic segmentation methods in the Avizo package could not separate the bones because they were not sufficiently distinct in density from the heterogeneous matrix, so segmenting was done by hand, highlighting each bone in two-dimensional views, with the area of bone marked every 10 slices. Once this process was completed along the entire length of a bone, the ‘interpolate’ function was used to fill the intervening spaces between the hand-drawn data areas. This two-dimensional slice information was then used to create a three-dimensional model of each bone. Seven of the bones were processed further by manually correcting each slice for poor interpolation, which was required especially for the detail of the vertebrae.

We explored several approaches to establishing the identity of the new archosaur. First, we coded characters for a full cladistic analysis of the new specimen against the substantial character list of Triassic archosaurs given by Ezcurra (2016), and using relevant taxa. We used PAUP (Swofford, 2003), deleting non-archosaurian and many basal archosauriform taxa as well as uninformative characters. We did not expect any resolution of the cladogram, because the preserved remains of Edgar do not include any confidently identified elements of the skull, pelvis, or hind limbs, so very few characters could be coded. Indeed, the analyses gave equivocal results (see Discussion for full details), and we consider other possibilities in view of the limited character coding from our new specimen.

In addition, we inspected other Pant-y-ffynnon and early crurotarsan material, in particular *Pantydraco* and *Terrestrisuchus*, to test whether any parts that had been assigned to Edgar by the UCL team in the 1950s might plausibly belong to any of the other Pant-y-ffynnon reptiles, or indeed any other taxon.

SYSTEMATIC PALEONTOLOGY

Subdivision ARCHOSAURIA Cope, 1869
Infradivision CRUROTARSI Sereno and Arcucci, 1990
Family ORNITHOSUCHIDAE Huene, 1908
AENIGMASPINA, gen. nov.

Type Species—*Aenigmaspina pantyffynnonensis*, sp. nov.

Diagnosis—As for species.

Etymology—From the Latin *aenigma*, meaning an enigma or puzzle, and *spina*, meaning spine. The generic name is thus a reference to the difficulty of recognizing the fossils referable to the animal and the problem of deciding its affinities, as well as

noting its key character of well-defined spine tables on anterior vertebrae.

AENIGMASPINA PANTYFFYNNONENSIS, sp. nov.
(Figs. 2–11)

Holotype—NHMUK P9/3a, consisting of two small complementary blocks containing 12 articulated or near-articulated anterior vertebrae, 12 ribs, eight osteoderms, one right scapula, and nine additional fragmentary bones (Fig. 2).

Referred Specimens—In addition to the holotype, we include three parts of humeri: NHMUK P9/3a, a right proximal end; NHMUK P9/2a, a left proximal end; and NHMUK P9/1a, a left distal end. Specimens probably referable to *Aenigmaspina* are a left scapula, a left humerus, and a left ulna recorded with the number NHMUK P50/4.

Diagnosis—A crurotarsan with a distinctive subrectangular spine table on the cervical and anterior dorsal vertebrae. Cervical vertebrae spine tables have anterior and posterior projections along their midline. Spine tables are found as far back as the fourth dorsal vertebra, and they show a deeply angled ‘V’ shape in anterior and posterior views, in which each half of the spine table is angled at up to 45° from the horizontal in cervical vertebrae; the more posterior spine tables have a more open ‘V’ shape, in which the two leaves of the spine table are closer to horizontal. No other described archosaur has such a deeply angled ‘V’-shaped spine table. The osteoderms bifurcate posteriorly and have a ventral longitudinal keel, thickened at the point of bifurcation, which attached precisely to a groove formed by the spine table. The scapula blade, straight in anterior and posterior views, is ca. 10–12 times as long as the narrowest width of the shaft and ca. 3.2–4.5 times as long as the greatest width of its proximal portion.

Etymology—The species name *pantyffynnonensis* refers to the quarry locality, Pant-y-ffynnon (Welsh; English translation ‘spring in a hollow’) in South Wales.

DESCRIPTION

In the description, we focus first on the core material of *Aenigmaspina*, comprising the two portions of a single block that contain the core skeletal elements, both of which are numbered P9/3a (Fig. 2A). We then consider the further three bones assigned the number P9/3a, and then the remainder of the *Aenigmaspina* referred material.

Block P9/3a—The two portions of P9/3a contain 12 vertebrae, 12 ribs, eight osteoderms, one scapula, and nine additional fragmentary bones, some of which can be assigned a probable identity. The cervical and dorsal vertebrae continue in sequence between the two separate blocks, confirming that they fit together as indicated (Fig. 2).

Vertebrae—We identify 12 vertebrae altogether, labeled A–L, in which A is most anterior and L is most posterior (Fig. 2B). Vertebrae A–C are cervicals and D–L are dorsals, based on the positions of the parapophyses and the diapophyses. Although it is common among archosaurs to have a continuum between the cervicals and the dorsals, these appear clearly differentiated and we cannot find any space for missing vertebrae within the A–L sequence. Assuming this archosaur had the primitive number of seven cervical vertebrae, we would then identify A–C as presacral vertebrae 5–7 and D–L as presacrals 8–17.

We describe four vertebrae in detail as representatives, namely, vertebrae B, E, H, and K, and consider first some general trends along the column. Vertebrae A–G possess a spine table, or expansion on the distal end of the neural spine. In the three preserved cervicals, the spine table (Fig. 2C) is equally large, roughly rectangular in shape in dorsal

view, and with the two halves sloping to a midline furrow that bears an anterior and a posterior projection that more or less touch the spine table in front and behind. Vertebra H has a bulge at the distal end, although it does not appear that material is missing, and vertebrae I–L have no indication of any broadening atop the neural spine. The diapophyses, which are level with the height of the centrum in anterior vertebrae, migrate dorsally and posteriorly throughout the sequence until they are level with the roof of the neural canal and just anterior of the postzygapophyses. The parapophyses undergo a similar movement, although it is constrained to the dorsoventral plane as the processes move from their position at the base of the centrum to mid-height of the neural canal. The centrum faces change shape from circular in the anterior vertebrae to dorsoventrally flattened in the more posterior examples.

Vertebra B—This is the middle cervical vertebra of the three preserved posterior cervicals. These three vertebrae are tightly articulated at the zygapophyses and are the most closely articulated of all the vertebrae (Fig. 2). In anterior view (Fig. 3A), the neural spine is vertical and the distal end expands into a spine table, which forms a ‘V’ shape at the top, marking a groove along the midline of the spine table. Below is the neural canal, which is large and about the same size as the centrum face, but more oval in shape, broader than high. The prezygapophyses (Fig. 3A) form broad plates, tilted about 45° inward, but not extending laterally beyond the margins of the neural canal. The centrum is circular, with a concave depression on the anterior face. In this view, the diapophyses (Fig. 3A) are visibly set out from the sides of the vertebra, positioned level with the top of the centrum, whereas the parapophyses, on the anterior margins of the centrum (Fig. 3A), barely protrude from the body of the centrum.

In left lateral view (Fig. 3B), the neural spine is located posteriorly, above the postzygapophyses, and it has a rectangular shape. The bone forming the lateral wall of the neural canal does not extend to the posterior edge of the centrum, creating a concavity between the postzygapophyses and the centrum when seen in lateral view (Fig. 3B). The lateral wall bears the zygapophyses (Fig. 3B). The diapophysis and the parapophysis can be distinguished on the anterior side of the centrum (Fig. 3B). The anterior and posterior faces of the centrum are aligned, without any hint of a vertical shift between the two. Along the ventral margin, the centrum is slightly excavated and the ventral keel is evident.

The posterior view (Fig. 3C) reveals that the spine table retains its width and ‘V’-shaped groove along the top, as in anterior view (cf. Fig. 3A). The posterior narrow margin of the neural spine expands ventrally to form the postzygapophyses, which slope inward at about 45°, so seemingly slightly steeper than the prezygapophyses. Between the postzygapophyses is a triangular depression above the roof of the neural canal. The canal and the centrum are equivalent in size and show the same shapes as on the anterior face (cf. Fig. 3A). The posterior face of the centrum is flat.

In dorsal view (Figs. 2C, 3D), the spine table is subrectangular, somewhat longer than wide. Its surface looks flat, but there is a longitudinal broad groove as the spine table forms a shallow ‘V’ shape (Figs. 2C, 3A, C). In ventral view, a pronounced keel is visible (Fig. 3E), confirming that this is a cervical vertebra. Further, the roughened bone around the anterior and posterior faces of the centrum forms broad areas in ventral view.

Vertebra E—This is the second dorsal vertebra and is loosely articulated with vertebrae D and F, having lost the tight articulation with its neighbors because of the curvature of the vertebral column, which creates gaps between otherwise adjacent bones (Fig. 2). In dorsal view (Fig. 3I), the spine table has shifted anteriorly in comparison with the cervical vertebra (cf. Fig. 3D) and

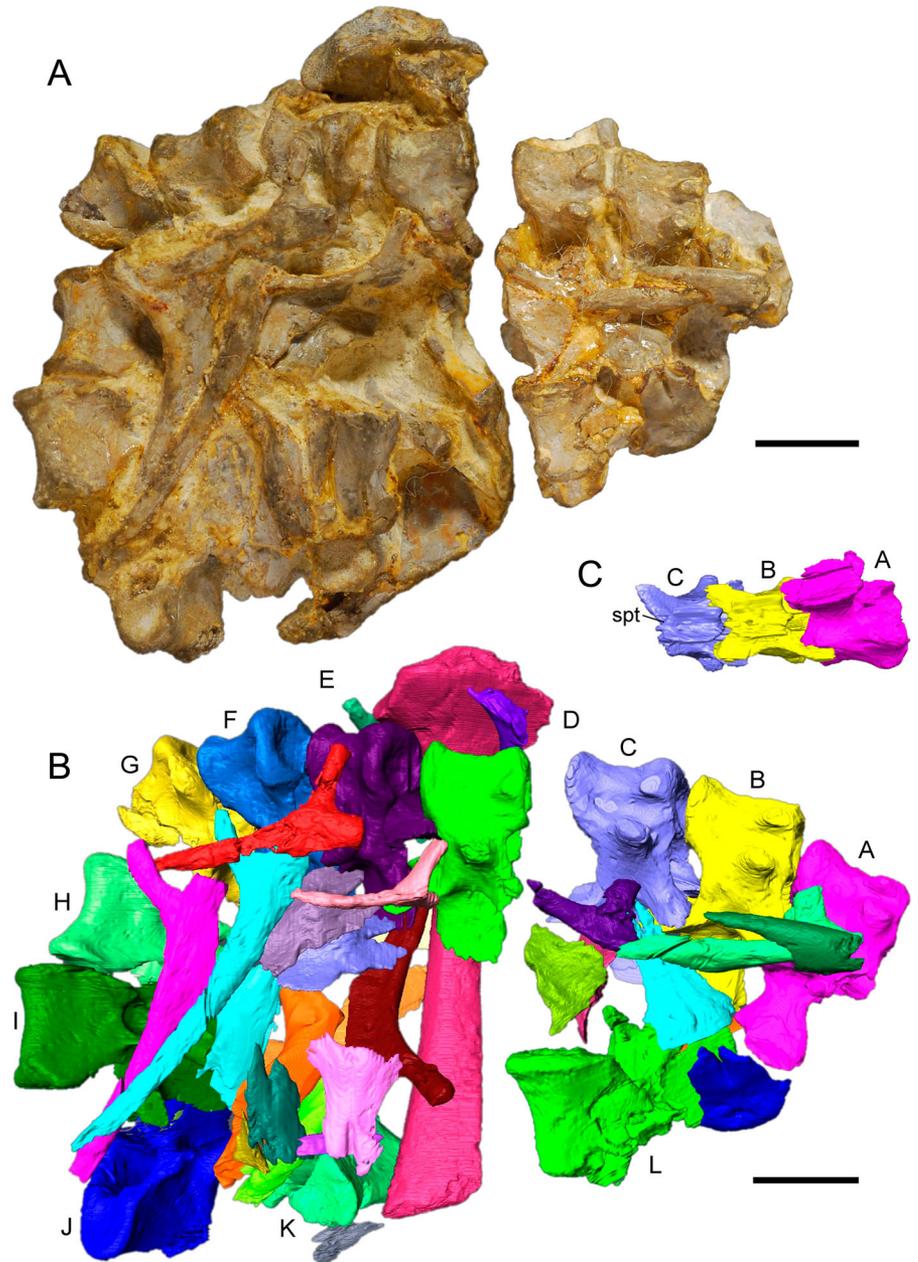


FIGURE 2. *Aenigmataspina pantyffynnonensis*, NHMUK P9/3a, core block in two pieces, placed together. **A**, specimen photograph and **B**, segmented 3D model of the included bones. **C**, detail of the three preserved cervical vertebrae, in dorsal view. Letters correspond to vertebrae ordered alphabetically from anterior to posterior. **Abbreviation:** spt, spine table. Scale bars equal 5 mm.

the diapophyses and zygapophyses project more markedly. The spine table has a straight anterior margin and a posterior margin with a midline point. In anterior view (Fig. 3F), vertebra E is squatter and wider than vertebra B in the same view (cf. Fig. 3A). The ‘V’ shape of the spine table (Fig. 3F) is less deep, the neural spine overall is shorter, and the prezygapophyses tilt inward at a higher angle. The neural canal (Fig. 3F) is wider than it is tall. The diapophyses project more markedly as rod-shaped structures, and the parapophyses are even less visible than on vertebra B (Fig. 3F). The diapophyses have also risen in position, resting midway up the lateral wall of the neural canal as opposed to adjacent to the centrum. The centrum is no longer circular in shape, but flattened on top, and with slight points on the lateral and ventral surfaces. The lateral points are the likely positions of the parapophyses, but the

vertebra lacks a keel, so the ventral point does not have a clear explanation.

In left lateral view (Fig. 3G), the neural spine is subrectangular in shape, with a slightly curved dorsal surface, and it lies more squarely above the centrum than in the cervical (cf. Fig. 3B). The zygapophyses and the neural canal lateral wall combine to make a posterior concavity; there is also a smaller concavity on the anterior and posterior sides of vertebra E, contrasting with the vertical anterior wall in the cervical (Fig. 3B). The diapophysis can be clearly distinguished on this side, but the parapophysis (Fig. 3G) is less well defined than on the cervical vertebra. The anterior and posterior faces of the centrum are level with each other, although the posterior face is shorter dorsoventrally than the anterior. The ventral surface of the centrum is more rounded than in the cervical.

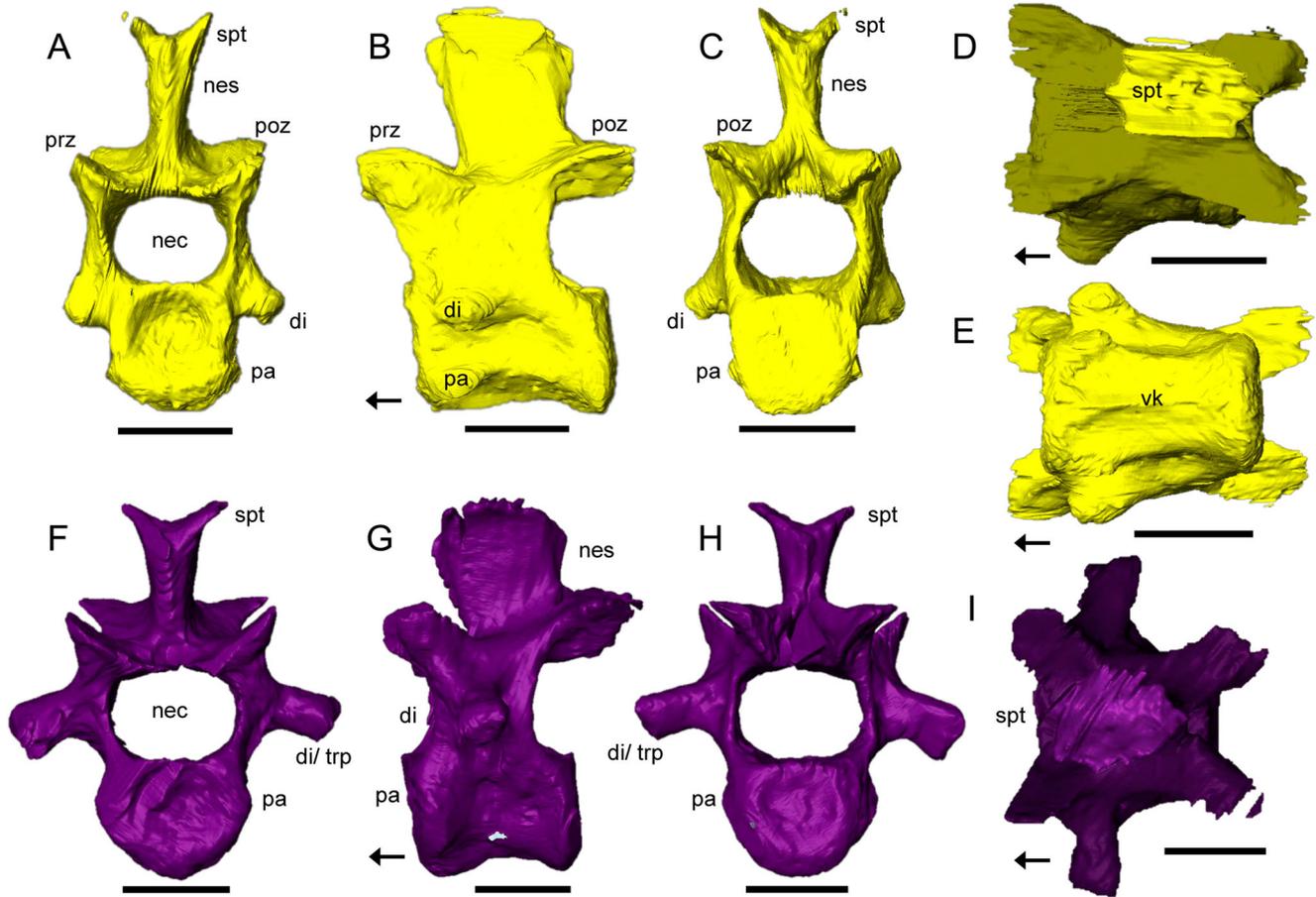


FIGURE 3. *Aenigmataspina pantyffynnonensis*, NHMUK P9/3a, mid-cervical and anterior dorsal vertebrae. **A–E**, vertebra B, mid-cervical in **A**, anterior, **B**, left lateral, **C**, posterior, **D**, dorsal, and **E**, ventral views. **F–I**, vertebra E, anterior dorsal in **F**, anterior, **G**, left lateral, **H**, posterior, and **I**, dorsal views. The spine table is highlighted in the dorsal views. Arrows indicate anterior direction. **Abbreviations:** **ce**, centrum; **di**, diapophysis; **nec**, neural canal; **nes**, neural spine; **pa**, parapophysis; **poz**, postzygapophysis; **prz**, prezygapophysis; **spt**, spine table; **trp**, transverse process; **vk**, ventral keel. Scale bars equal 3 mm.

The posterior view (Fig. 3H) offers the best view of the parapophyses, which appear as slight bulges halfway up the side of the centrum. The proportions of all parts are similar to those in the anterior view (Fig. 3F), showing the shorter neural spine, larger neural canal, smaller centrum, steeper-sloping postzygapophyses, and more developed diapophyses, which project laterally and slope downward as distinctive rod-like transverse processes (Fig. 3F, H). The dorsal view (Fig. 3I) shows the somewhat shield-shaped spine table, straight edge anterior and point posterior.

Vertebra H—This is the fifth dorsal vertebra in the preserved sequence and is semiarticulated with vertebra I. There is a gap between vertebrae G and H, but not large enough that a vertebra is missing, which is confirmed by matching ribs to vertebrae. The anterior view (Fig. 4A) demonstrates a different overall vertebral shape from the previous examples, even with the right diapophysis missing. The neural spine appears taller because there is no spine table, merely a slight distal expansion. The prezygapophyses (Fig. 4A) tilt inward at a steep angle, about 60°. The neural canal (Fig. 4A) is more equal in its width and height proportions than in vertebra E and is thus more like vertebra B (cf. Fig. 3A, F). The diapophysis/transverse process (Fig. 4A, B) has moved further dorsally, now protruding from level with the top of the neural canal; it projects upward, rather than downward as in the anterior dorsal (cf. Fig. 3F). The centrum is broader

along the dorsal side than the ventral, giving a rounded trapezoid shape as compared with the circular disc from more anterior bones. The center is concave.

The left lateral view (Fig. 4B) shows a rectangular neural spine positioned far back over the postzygapophyses. This view clearly shows the diapophysis on the same level as the zygapophyses and demonstrates that the parapophysis (Fig. 4B) has moved dorsally as well, forming part of the lip of the anterior face of the centrum and being located more dorsally than in the anterior dorsal (cf. Fig. 3G). The concavity of the neural canal's lateral wall is quite pronounced posteriorly and minimal, although present, on the anterior side. Unlike the previous vertebrae (cf. Fig. 3B, G), the dorsal curvature of the ventral margin of the centrum is pronounced.

The posterior view (Fig. 4C) shows the neural spine and broadly divergent postzygapophyses (Fig. 4C), forming a deep triangular depression between. The diapophyses are long, rod-like processes sloping slightly upward distally (Fig. 4C), and the parapophyses, as in earlier examples, are clearly visible and appear well pronounced on the upper shoulders of the centrum. The posterior face of the centrum is like a square with rounded corners in outline, and it is slightly concave.

Vertebra K—The eighth dorsal vertebra, vertebra K, does not articulate with any of its neighbors. Vertebrae J and K are rotated 90° from their closest neighbor, vertebra I, and vertebra L is

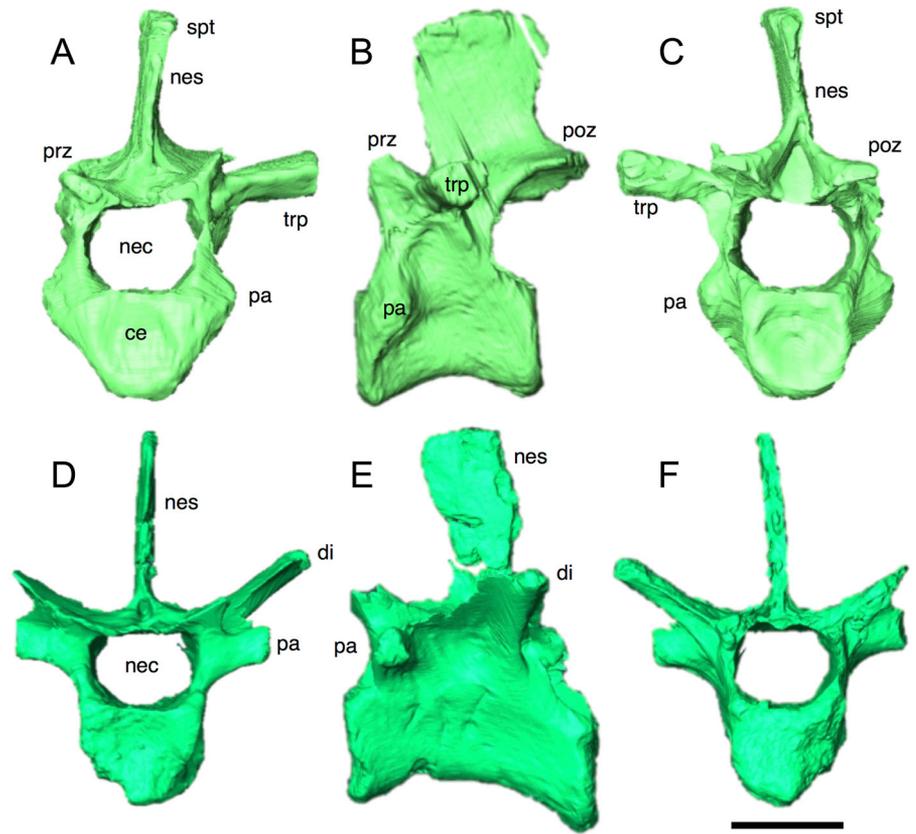


FIGURE 4. *Aenigmataspina pantyffynnonensis*, NHMUK P9/3a, mid-dorsal vertebrae H (A–C) and K (D–F). A–C, vertebra H in A, anterior, B, left lateral, and C, posterior views. D–F, vertebra K in D, anterior, E, left lateral, and F, posterior views. Anterior is on the left in B and E. **Abbreviations:** ce, centrum; di, diapophysis; nec, neural canal; nes, neural spine; pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis; spt, spine table; trp, transverse process; vk, ventral keel. Scale bar equals 3 mm.

located on the smaller block. The anterior view (Fig. 4D) shows a tall, thin neural spine with no hint of distal expansion (Fig. 4D). At the base of the neural spine is an oval depression that has not been found on the other vertebrae. The diapophyses project upward at about 45°, and they are long. The parapophyses are more pronounced than they have been previously and rise dorsally to the middle of the neural canal, making the prezygapophyses look small and the lateral walls of the neural canal quite thick in comparison with those of more anterior vertebrae. The neural canal (Fig. 4D) appears slightly dorsoventrally compressed, as in vertebra E (cf. Fig. 3F). The centrum is slightly incomplete ventrally, but the dorsal margin is straight.

The left lateral view (Fig. 4E) shows a subrectangular neural spine set in the posterior half of the vertebra, and in which the anteroposterior width is shorter than in any of the other vertebrae, but this posterior margin was damaged before burial, removing the postzygapophyses as well. The diapophysis and the parapophysis are clear and protruding (Fig. 4E). There is a thin lamina of bone apparently connecting the anteriorly located parapophysis and the posteriorly located diapophysis, but this is damaged. The centrum is much longer than in more anterior vertebrae, and for the first time in this sequence the posterior face of the centrum lies ventral to the anterior face, creating a strong curve in the ventral surface of the centrum. This vertebra shows much greater dorsoventral compression between the zygapophyses and the base of the centrum than has been seen earlier in the sequence.

In posterior view (Fig. 4F), the tall, thin neural spine shows evidence of damage to its posterior margin, and absence of the postzygapophyses. The diapophyses project laterally and diagonally dorsolaterally, whereas the parapophyses are shorter, deeper, and more horizontal. The neural canal is roughly circular, as is

the posterior face of the centrum, but the centrum margin comes to a slight point ventrally.

Ribs—The NHMUK P9/3a blocks contain three long ribs, nine short ribs, and six fragments that may be ribs, and where rib heads are present, all are dichoccephalous (Fig. 5). Although none of the ribs articulates perfectly, six ribs (seven when including a fragment) can be assigned to their corresponding vertebra based on their positions. Two of these ribs and the one fragment are identified as cervical ribs because of their morphology and their position alongside the cervical vertebrae. These cervical ribs articulate with vertebrae B and C, and the fragment articulated with vertebra A. The identification of these three as cervical ribs is confirmed by their shape, in which the tuberculum and the capitulum extend orthogonally from the rib shaft, parallel to one another, and the distal projection of the rib is short. This matches the relation of the diapophysis and the parapophysis, which are distinct but nearly touching in the corresponding cervical vertebrae.

Vertebrae D and E nearly articulate with short ribs, and vertebrae F and G nearly articulate with long-shafted ribs. The change in size of the ribs across vertebrae D–G demonstrates a transition between cervical and dorsal vertebrae. The rib associated with vertebra D is particularly important, because neither the tuberculum nor the capitulum lies along the plane of the shaft but both are at an angle that is no longer orthogonal as in the cervical ribs. In addition, the two heads are not parallel to one another as they are in the cervicals. The rib connected to vertebra E then shows a more standard dorsal rib shape in which the tuberculum is an extension of the shaft and the capitulum lies at an angle to both pieces, yet the shaft is short. The rib heads associated with vertebrae F and G have similar shapes, although the capitulum changes shape to accommodate the migrating position of the parapophysis and the rib shaft extends more posteriorly.

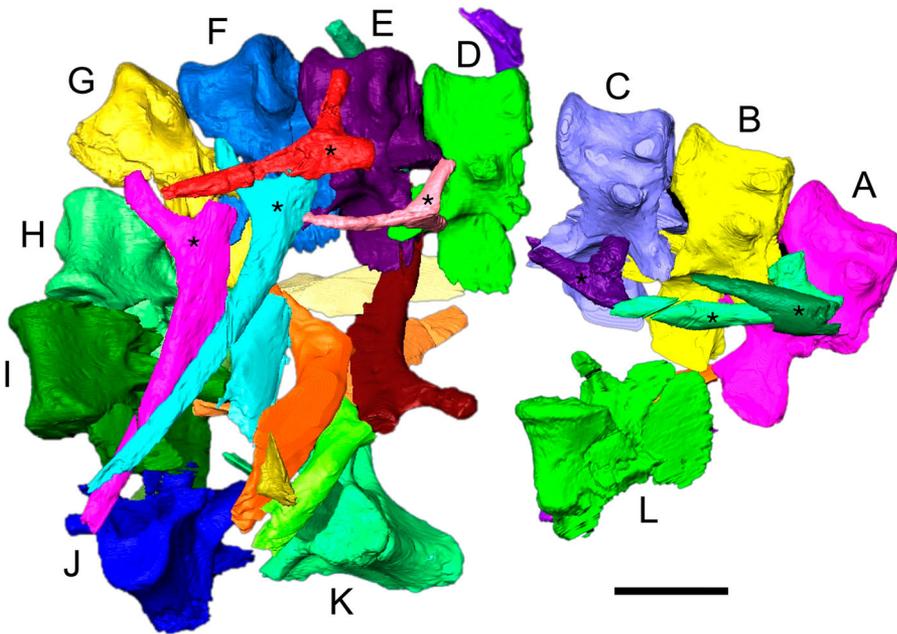


FIGURE 5. *Aenigmataspina pantyffynnonensis*, NHMUK P9/3a., vertebrae and ribs (including fragments). Letters correspond to vertebrae, in order from front to back. Ribs discussed in the text are noted by *. Scale bar equals 5 mm.

Scapula—The right scapula is relatively complete, lacking just the distal end of the blade and being damaged on the anterior margin of the proximal portion (Figs. 1, 6). The scapula is long and slender, measuring 29 mm in maximum proximal–distal length, 9 mm wide at most at the ventral end, and with a blade that is 5 mm wide distally and 2.8 mm at the narrowest part. The blade is therefore 10 times as long as the narrowest width of the blade and 3.2 times as long as the greatest width of its ventral portion. In lateral view (Fig. 6B), the anterior and posterior margins of the scapula shaft are remarkably straight and the dorsal end terminates in a straight margin that appears to be incomplete, perhaps having passed into cartilage rather than having been broken. The blade margins curve symmetrically ventrally, because the blade expands anteriorly and posteriorly. The anterior margin and the acromion process (Fig. 6B) were removed by damage, but the curved margin for contact with the coracoid is complete. The glenoid (Fig. 6A, B) is angled at about 20° above the horizontal and so faces largely ventrally and only a little posteriorly. The glenoid is supported above by a columnar portion of the posterior margin of the ventral scapular region that bears some irregularities that could be muscle scars representing the origin of the triceps longus lateralis. In crocodylians, this muscle (Meers, 2003:fig. 3) attaches to the scapula via a long tendon that leaves a prominent scar in this location above the glenoid and it inserts on the olecranon process of the ulna and assists in extending the ulna during locomotion.

The scapular blade is straight in anterior and posterior views (Fig. 6A, C), without much curvature around the flanks of the animal and running essentially straight from proximal to dorsal. Proximally, the scapula thickens toward the glenoid and the coracoidal margin. The glenoid (Fig. 6A) is deeply excavated to accommodate the proximal head of the humerus and is overall roughly square in outline.

Osteoderms—There are nine osteoderms in the two blocks, four in the small block and five in the large one, of which one is a fragment (Figs. 2, 5, 7). The osteoderms are thin and flat, and they vary slightly in size, measuring 5.5–6.5 mm long and 4.0–4.5 mm wide at the maximum point. Osteoderm shape seems constant over the block, although it cannot be said for sure whether

the osteoderms lie close to their original locations in the body, whether they are osteoderms over the neck in the small block (Fig. 7A–D), or osteoderms over the anterior portion of the trunk in the larger block (Fig. 7E, F). The osteoderms with a



FIGURE 6. *Aenigmataspina pantyffynnonensis*, NHMUK P9/3a. Right scapula in A, posterior, B, lateral, and C, anterior views. **Abbreviations:** **acr.** acromion process; **gl.** glenoid. Scale bar equals 5 mm.

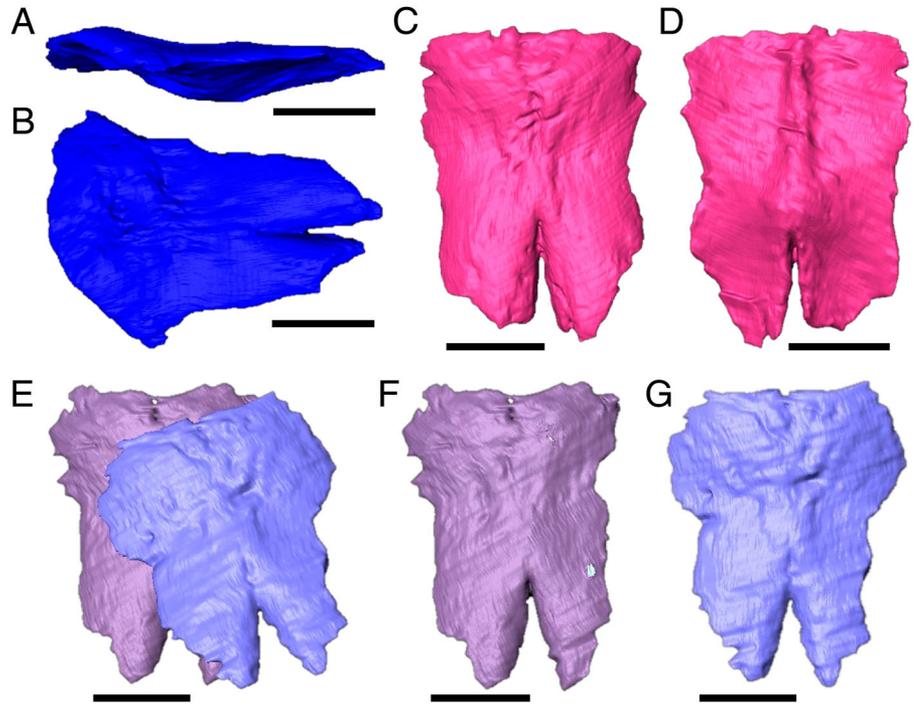


FIGURE 7. *Aenigmaspina pantyffynnonensis*, NHMUK P9/3a, osteoderms. **A**, **B**, anterior osteoderm in **A**, lateral and **B**, dorsal views. **C**, **D**, anterior osteoderm in **C**, dorsal and **D**, ventral views. **E–G**, ventral views of osteoderms that lie close to dorsal vertebrae **E** and **F**, showing osteoderms as **E**, preserved in situ and **F**, individually. Gray spot on **F** is an artifact of 3D visualisation. Anterior is toward the top, except in **A** and **B** in which it is to the left. Scale bars equal 2 mm.

straight anterior edge (e.g., Fig. 7E, F) are more rectangular than those with a rounded anterior edge (Fig. 7B).

The anterior margins of the osteoderms (Fig. 7) are straight or rounded, whereas the posterior end most often separates into two swallowtail processes. These posterior processes can come to narrow points or have more blunted ends in different osteoderms, although the blunt ends might have resulted from damage. In one osteoderm, the posterior projections make up half the length of the osteoderm.

The osteoderms bifurcate posteriorly, suggesting possible fusion of paired plates. Fusion cannot be demonstrated here, however, because the computed tomography (CT) scans do not allow enough discrimination at this small scale. However, at the anterior margin in one specimen (Fig. 7E, F), there is an apparent spiked, overlapping suture line in the midline, seen also in the associated osteoderm (Fig. 7E, F) as a smaller notch at the midline of the osteoderm anterior margin. In other archosaurs, osteoderms are generally paired, except for the first one behind the skull, but the proterochampsians *Chanaresuchus* and *Tropidosuchus* each have a single column of osteoderms dorsal to the vertebral column (Nesbitt, 2011).

The ventral side of the osteoderms (Fig. 7D) displays a slightly arched mediolateral convexity or ridge that runs longitudinally from the anterior end to the bifurcation of the posterior processes. The linear convexity is not constant in size but swells near the point of bifurcation, expanding both in ventral depth and mediolateral thickness. The linear convexity fits precisely into the broad groove, or ‘V’-shaped furrow, observed on top of the neural spine tables of the vertebrae (e.g., Fig. 3A, C, F, H).

The osteoderms bear minimal sculpture, and it is important not to confuse the linear scan artifacts for sculpture (Fig. 7A–C, E, F). Behind the putative midline suture at the anterior margin (Fig. 7E, F), there are some irregular, bulbous sculpture marks at the high point of the osteoderm, with further markings laterally over the waisted area anterior to the posterior bifurcation.

Whether osteoderms were restricted to the neck region and anterior-most trunk, as suggested by the absence of spine tables

on certain vertebrae (e.g., Fig. 4A, D), cannot be confirmed. Such a restriction to the location of the armor is unusual among Triassic archosaurs, most of which have osteoderms extending along the length of the vertebral column, from behind the skull to the tail (Nesbitt, 2011; Ezcurra, 2016). On the other hand, the ornithosuchids *Ornithosuchus* and *Riojasuchus* and the rauisuchid *Prestosuchus* have only presacral osteoderms, as most likely is the case in our specimen.

Additional Elements

Humerus—Among the closely associated elements are three portions of humeri: a right proximal end (Fig. 8A, B), a left proximal end (Fig. 8C, D), and a left distal end (Fig. 8E, F), numbered P9/3a, P9/2a, and P9/1a, respectively. The two proximal ends are of the same size, each 15 mm long, and the distal end matches in size, being maximally 10 mm wide, corresponding to the 12-mm-wide proximal ends. The proximal end shows the articular condyles (Fig. 8A–D) and the deltopectoral crest (Fig. 8A–D), which is a rounded structure, expanding slightly on the anterior margin, located close to the proximal end, and neither extending down the shaft nor expanded into a projecting process. The distal end of the humerus shows the supinator process (Fig. 8E, F) on the ectepicondylar side as a rounded boss. The very clear trochlea at the distal end shows separate radial and ulnar condyles (Fig. 8E, F). The shapes of these elements are like those of other Late Triassic slender, small crurotarsan archosaurs such as *Erpetosuchus* (Benton and Walker, 2002:fig. 6) in having a well-defined articular condyle for insertion into the scapulocoracoid glenoid and a slightly downturned deltopectoral crest close to the proximal end of the humerus (Fig. 8A–D). These specimens differ from the humerus of *Terrestriisuchus* (Crush, 1984: fig. 7) in being broader and without the triangular deltopectoral crest, and from that of *Pantydraco* (Galton and Kermack, 2010: fig. 17) in having a much narrower proximal end and more proximally located deltopectoral crest.

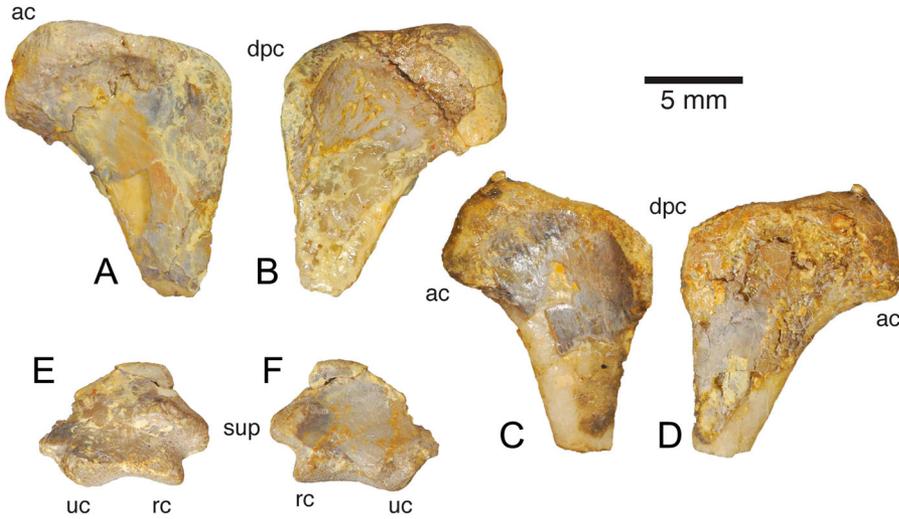


FIGURE 8. Specimens of *Aenignaspina pantyffynnonensis* with numbering that associates them with the type specimen (NHMUK P9/3a, P9/2a, P9/1a, respectively). **A, B**, right humerus, proximal end, in **A**, lateral-dorsal and **B**, medial-ventral views. **C, D**, left humerus, proximal end, in **C**, lateral-dorsal and **D**, medial-ventral views. **E, F**, left humerus, distal end, in **E**, lateral-dorsal and **F**, medial-ventral views. **Abbreviations:** **ac**, articular condyle; **dpc**, deltopectoral crest; **rc**, radial condyle; **sup**, supinator process; **uc**, ulnar condyle.

The other numbered P9/3a specimens, a narrow-sided vertebra and a possible left scapula in two pieces, are too damaged to illustrate or describe.

Vertebrae—The collection includes 20 vertebrae, some in pairs and threes, but most now isolated and removed from the rock. In determining whether these might plausibly belong with the core pieces of *Aenignaspina*, we compared the specimens for size and anatomical characters, and they all matched convincingly. We illustrate and describe only the more complete specimens here (Fig. 9). These, and the other 17 vertebrae, match those in the type block in terms of preservation and sediment, as well as in anatomy and size. The first vertebra to be described, NHMUK RU P44/3 (Fig. 9A–D), is 10.5 mm tall and shows the spine table that slopes at some 30° below horizontal posteriorly and all the

other features seen in the scanned mid-cervicals (cf. Fig. 3A–E), so it could be a specimen removed from the type series. The second vertebra, NHMUK P26/9 (Fig. 9E, F), is slightly larger, being 11.5 mm tall and 10.5 mm across the transverse processes, but although it lacks the projecting spine table it still has a broad dorsal expansion of the neural spine. The size and broad, horizontal transverse processes suggest that this is a mid-dorsal. The caudal centrum, NHMUK P26/18 (Fig. 9G), is 7.5 mm long, slightly bowed ventrally, and mediolaterally thin.

Scapula and Forelimb from Another Individual—There are some complete forelimb elements that are from a different individual from the type series, the anatomy of which appears to be identical to that of *Aenignaspina*. We know that this is another animal because there are duplicated elements, viz., the left

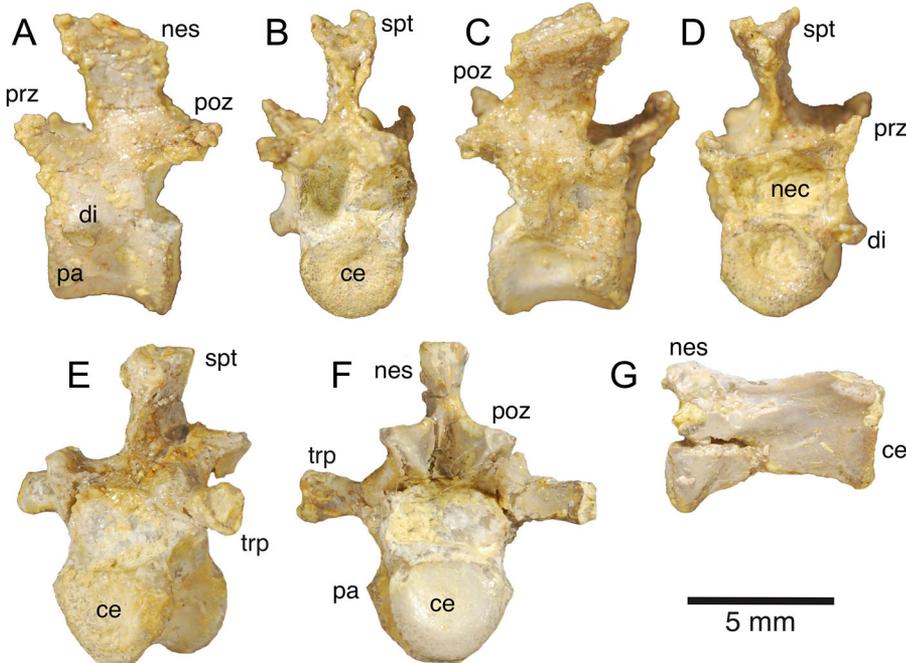


FIGURE 9. Possible vertebrae of *Aenignaspina pantyffynnonensis* that match in size and morphology those scanned in the type block (cf. Figs. 2–4). **A–D**, mid-cervical vertebra NHMUK RU P44/3 in **A**, left lateral, **B**, posterior, **C**, right lateral, and **D**, anterior views. **E, F**, mid-dorsal vertebra NHMUK P26/9 in **E**, anterolateral and **F**, posterior views. **G**, caudal vertebra NHMUK P26/18 in right lateral view. **Abbreviations:** **ce**, centrum; **di**, diapophysis; **nec**, neural canal; **nes**, neural spine; **pa**, parapophysis; **poz**, postzygapophysis; **prz**, prezygapophysis; **spt**, spine table; **trp**, transverse process; **vk**, ventral keel.

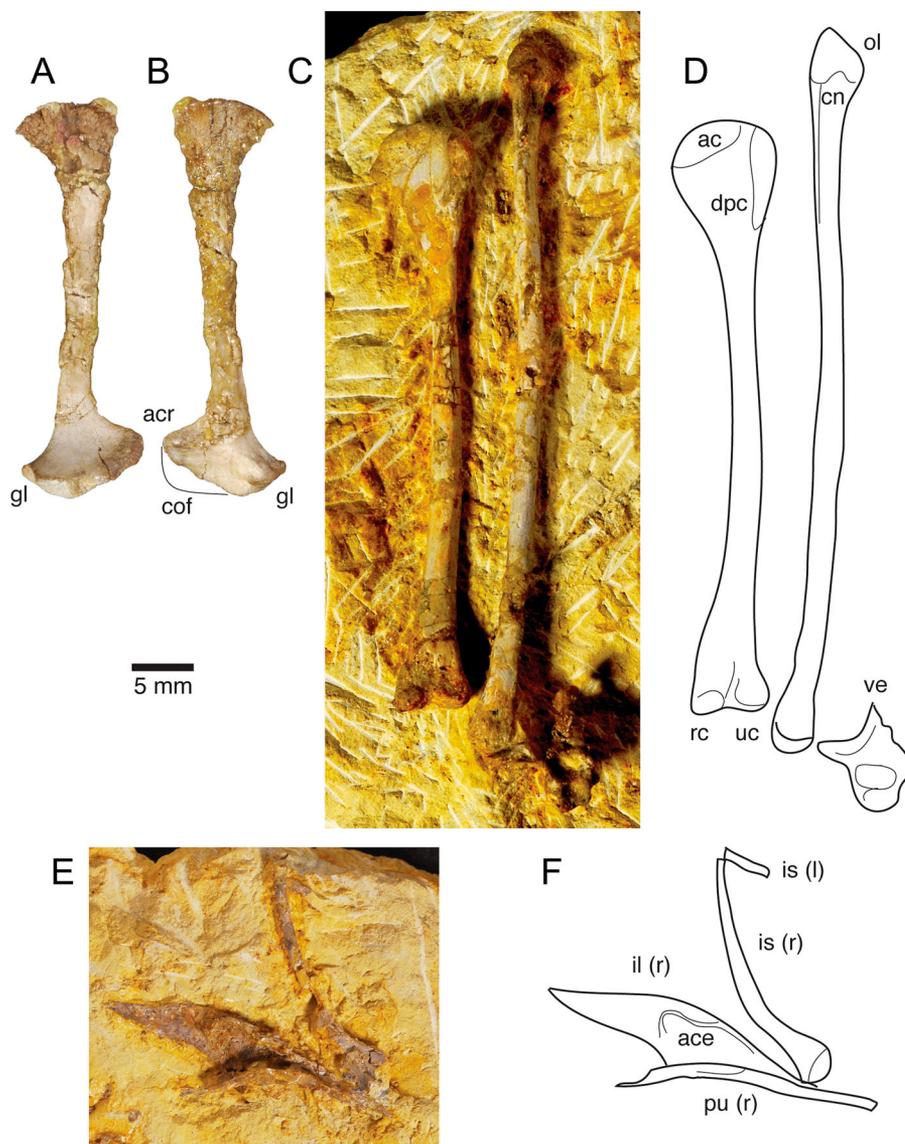


FIGURE 10. Possible limb bones of the same species as *Aenigmataspina pantyffynnonensis*, but a different individual. **A–D**, prepared specimens, all numbered NHMUK P50/4, and so likely found on a single block. **A, B**, left scapula in **A**, medial and **B**, lateral views, with blade uppermost. **C**, photograph and **D**, interpretive drawing of associated left humerus, ulna, and isolated vertebra. **E**, photograph and **F**, interpretive drawing of NHMUK P26/17, a right pelvis with ilium, ischium, and pubis slightly perturbed, but associated. **Abbreviations:** **ac**, articular condyle; **ace**, acetabulum; **acr**, acromion process; **cn**, cnemial crest; **cof**, coracoidal facet; **dpc**, deltopectoral crest; **gl**, glenoid; **il**, ilium; **is**, ischium; **l**, left; **ol**, olecranon; **pu**, pubis; **r**, right; **rc**, radial condyle; **uc**, ulnar condyle; **ve**, vertebra.

humerus. However, as well as sharing identical anatomy where elements may be compared (scapula, proximal end of humerus), the sizes and enclosing sediment are identical. All elements have the same number, NHMUK P50/4.

The left scapula (Fig. 10A, B) is 36 mm long, compared with the type scapula which is 29 mm long (cf. Fig. 6). The scapula comprises a long blade, maximally 8 mm wide at the top and minimally 3 mm wide at the narrowest portion of the shaft, and the blade is 4.5 times its maximum width and 12 times its minimum width. The upper end of the blade is curved upward, and the blade flares mostly backward. Most of the blade is narrow, and is flattened, and then expands rapidly at the ventral end to support a strong upper portion of the glenoid for articulation of the humerus, as well as for the contact with the coracoid (Fig. 10A, B), which is missing. The glenoid facet (Fig. 10A, B) is 5 mm wide, measured mediolaterally. The acromion is a rounded expansion on the anterior margin close to the ventral end (Fig. 10A, B).

The preservation of the left humerus and ulna in a single block (Fig. 10C, D) is unusual, and likely the scapula was removed from

this block, which has been much prepared. Both elements are long and slender. The humerus is 53 mm long, maximally 11 mm wide at the proximal end and 7 mm at the distal end. It is preserved in ventral (posterior) view (Fig. 10C, D) and shows the articular condyle and the deltopectoral crest at the proximal end and the radial and ulnar condyles at the distal end.

The left ulna is longer than the humerus, at 64 mm long and representing 121% of humerus length. The proximal end of the ulna, with the olecranon, lies beside the proximal end of the humerus (Fig. 10C, D), confirming that the forelimb is not articulated, in which case the olecranon would sit beside the distal end of the humerus. The olecranon (Fig. 10D) is short, 4 mm long, and a cnemial crest (Fig. 10D) runs down the shaft for some 12 mm. The shaft is 2.5–3 mm in diameter in all orientations, and the distal end is only slightly expanded.

These elements are similar in proportions to those of *Terrestri-suchus* (Crush, 1984:fig. 7), but the scapula is more slender and with a narrower distal expansion of the blade. Further, the deltopectoral crest of the humerus is more proximally located and is not triangular, as in *Terrestri-suchus*. The ulna is very similar,

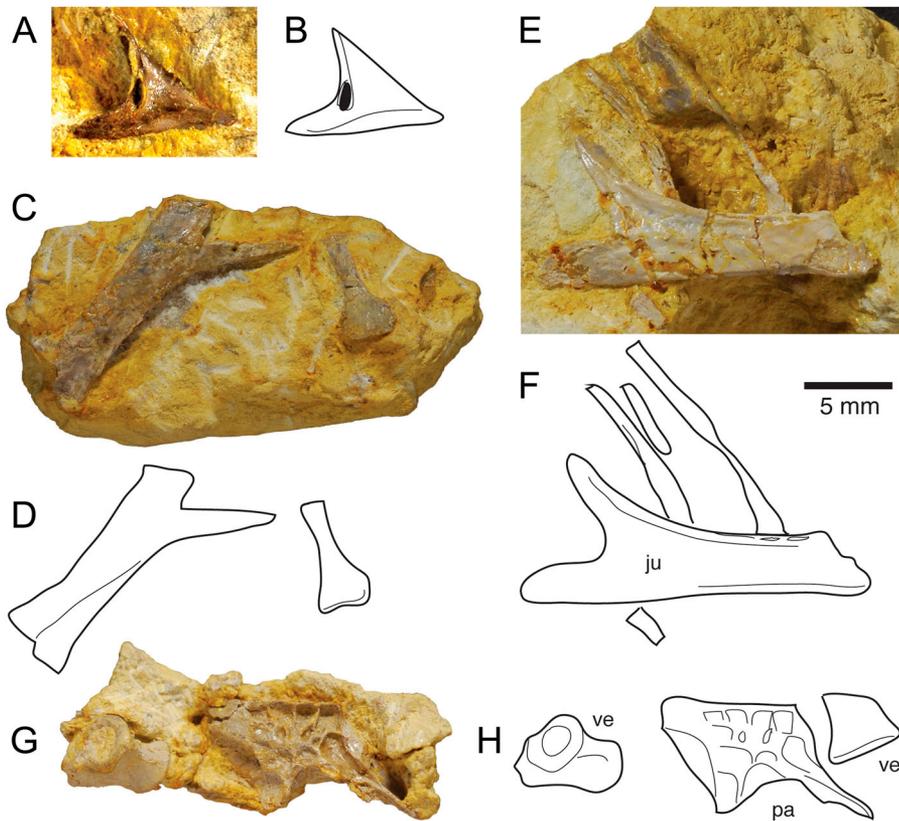


FIGURE 11. Photographs and interpretive drawings of skull elements possibly attributable to *Aenigmaspina pantyffynnonensis*. **A, B**, NHMUK PV RU P50/4, possible lacrimal. **C, D**, NHMUK B P50/4, possible jugal. **E, F**, NHMUK RU P51, right jugal and two vertebrae. **G, H**, NHMUK P26/41, heavily sculptured left parietal. **Abbreviations:** ju, jugal; pa, parietal; ve, vertebra.

however. The humerus of *Pantydraco* is much shorter and has broader ends, and the scapula and the ulna are incompletely known (Galton and Kermack, 2010:fig. 17). The fact that the humerus lacks the supinator process at the distal end and the articular condyles and deltopectoral crest are less developed than in the type specimen (Fig. 7) might suggest that this is from a juvenile. If so, it would be a considerably larger animal than the type of *Aenigmaspina*.

Pelvis Possibly from This Taxon—The type material of *Aenigmaspina* does not include any portions of the posterior part of the skeleton. One small block of yellow sediment, identical in appearance to everything yet described (NHMUK P26/17), has been allocated to Edgar in the collection records, but we cannot test this further. However, we present this here because it is neither *Terrestriusuchus* (which is twice the size [the pubis is 50 mm long] but the ilium is of similar shape; Crush, 1984:fig. 8) nor *Pantydraco* (ilium stocky and posterior process is short and square in section; pubis and ischium also shorter and thicker; Galton and Kermack, 2010:fig. 19).

The posterior part of the right ilium is visible (Fig. 10E, F), showing a sharply pointed posterior process, extending 9.5 mm behind the deep acetabulum. Its anterior portion is partly overlain by the right pubis, which is a slender element, of which some 21 mm are preserved. Likewise, the right ischium is also out of place, some 20 mm long, and with an expanded proximal portion. A small portion of a possible left ischium is also visible (Fig. 10E, F). Regrettably, all three elements are in poor condition, having been delicate and subjected to needle preparation.

Skull Elements Possibly from This Taxon—The final cluster of bones comprises dermal skull elements (Fig. 11), but whether from *Aenigmaspina* or some other archosaur is unclear. They are all stored and numbered in sequence with the *Aenigmaspina*

remains. Some, such as the possible lacrimal (Fig. 11A, B), identified by the large lacrimal foramen, are part of NHMUK PV RU P50/4. This is in a small block of sandy limestone that has been cut and substantially prepared, with signs that other items have been removed from the block, as with other blocks bearing the same number.

Two specimens might represent jugals. The first, NHMUK B P50/4 (Fig. 11C, D), contains two slightly damaged elements, and it is unclear to what extent the shape of the larger one is original or has emerged during preparation. Another specimen (NHMUK RU P51) is in better condition and is labeled as containing a ‘right jugal and lacrimal?’; certainly the putative jugal (Fig. 11E, F) has the characters of this element, with the broad, curved sweep marking the ventral margin of the orbit, a broken anterior end that would have contacted the maxilla, and a bifurcating posterior portion with the pointed posterodorsal process to contact the postorbital and the posterior process ending in a rounded lappet that might have contacted the quadratojugal. If so, this indicates a complete lower temporal bar. If this is a jugal, it is different in shape from the narrow jugal of *Erpetosuchus*, which bears a transverse ridge separating two lateral faces (Benton and Walker, 2002:fig. 2a).

The final skull element is the left parietal, associated with two partial vertebral centra, NHMUK P26/41 (Fig. 11G, H). The parietal is a delicate element, 9 mm long along the putative midline, showing a curving margin for the upper temporal fenestra, extending into the narrow posterolateral process that comes to a point as it rotates to a vertical orientation, forming the facet for articulation with the squamosal, all features of the squamosal of most archosaurs (Nesbitt, 2011). The parietal is deeply sculptured, showing seven or eight square-sided depressions, surrounded by narrow, crested walls. This element is flatter than

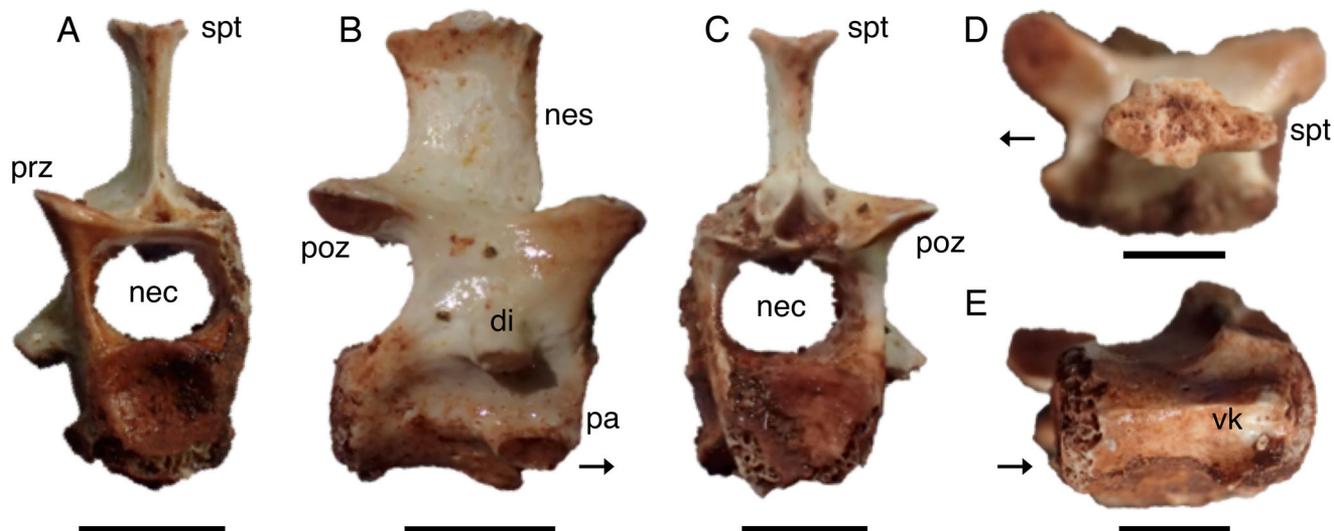


FIGURE 12. NHMUK PV R37263, vertebra of an undescribed Cromhall Quarry crurotarsan, in **A**, anterior, **B**, right lateral, **C**, posterior, **D**, dorsal, and **E**, ventral views. Arrows indicate anterior direction. **Abbreviations:** *di*, diapophysis; *nec*, neural canal; *nes*, neural spine; *pa*, parapophysis; *poz*, postzygapophysis; *prz*, prezygapophysis; *spt*, spine table; *vk*, ventral keel. Scale bars equal 4 mm.

the parietal of *Erpetosuchus*, which slopes down laterally and apparently has no sculpture (Benton and Walker, 2002:fig. 2b).

Vertebra from Cromhall—There is an isolated cervical vertebra of an unknown archosaur from Cromhall Quarry that is like those of *Aenigmaspina* (NHMUK PV R37263; Fig. 12). The spine table (Fig. 12A, C, D) is damaged, so the shape is hard to make out, but its presence is consistent with *Aenigmaspina*, and the anterior and posterior views demonstrate that the top of the table presents a concavity as in vertebra B (Fig. 3A–E). The shapes of the neural canal, centrum face, and centrum body, as well as the location of the transverse processes, all match those of *Aenigmaspina*. The neural spine is rectangular in right lateral view and positioned more toward the posterior end of the vertebra. The keel, as seen in ventral view (Fig. 12E), indicates that this is a cervical vertebra, matching what is seen in *Aenigmaspina*.

DISCUSSION

Preservation of Specimen P9/3a

The overall structure of P9/3a is curious because the vertebrae are in an almost continuous sequence, with ribs, osteoderms, and a scapula in near-articulation positions (Fig. 1), and yet the animal is curled up tightly. We have considered several possibilities to account for these features. One suggestion is that the fossil derived from a predator's regurgitated pellet, but the bones seem to approximate their life positions, so it is unlikely that they were churned in a predator's guts. It is known that large Late Triassic predators consumed their prey whole and passed coprolites or produced regurgitates containing abundant bones and teeth (Qvarnström et al., 2019), but in these particular examples the bones are entirely disarticulated, and broken and crushed, unlike the appearance of the *Aenigmaspina* remains. A second possibility is that the animal was an embryo that died while still in the egg but the eggshell was not preserved, or a hatchling that had left the egg but died in a curled-up posture. However, there are no clear juvenile traits on the holotype such as unfused neural arch and centrum, and the estimated overall length of the individual, at least 45 cm, is rather large for a hatchling. The final possibility we considered is that the animal was

coiled up in a burrow, dying there and either found in situ or the tightly coiled carcass was transported a short distance.

Phylogenetic Position within Archosauriformes

Before proceeding to the phylogenetic analysis, we tried to narrow down the clades to which *Aenigmaspina* might belong, because many available cladistic data matrices include a wide range of archosauromorph taxa, and with limited coding, we wanted the analyses to run to completion. We began with what had long been assumed, namely, that *Aenigmaspina* was an archosaur and a crurotarsan. Further, we focused on the holotype (Fig. 2), unless otherwise stated, so as to avoid the risk of confounding characters of a possible chimera.

We can identify *Aenigmaspina* as an archosauriform because it lacks postaxial intercentra (Benton and Clark, 1988; character 177 of Nesbitt, 2011; character 346 of Ezcurra, 2016) and the acromion process in the scapula is located well above the ventral edge of the element (character 220 of Nesbitt, 2011). Further, the presence of osteoderms is generally seen as an archosauriform character (character 401 of Nesbitt, 2011; character 588 of Ezcurra, 2016). The osteoderms of *Aenigmaspina* do not seem to match those of any other described archosaur, and yet they also do not show any of the characters listed as diagnostic of clades (Nesbitt, 2011; Ezcurra, 2016).

Most diagnostic apomorphies of crown Archosauria (= Avesuchia; Benton, 1999) cannot be assessed in *Aenigmaspina*, in that it lacks skull elements, coracoid, metacarpals, and hind limbs. However, if the humeri described here (Figs. 8, 10) belong to the same taxon, they show two characters of crown Archosauria: the humerus with a medially expanded proximal end, being asymmetric in anterior view (character 419 of Ezcurra, 2016), and the proximal articular surface separated by a gap from the deltopectoral crest (character 233 of Nesbitt, 2011; character 418 of Ezcurra, 2016). Furthermore, the olecranon process of the ulna of NHMUK P50/4 (Fig. 10C, D) is prominent, but lower than its anteroposterior depth at the base, which is a possible crown archosaur apomorphy (character 430 of Ezcurra, 2016).

We tested whether *Aenigmaspina* could be a member of Avemetatarsalia, especially in light of the expansion of that clade to include Aphanosauria (Nesbitt et al., 2017). *Aenigmaspina* lacks

key avemetatarsalian apomorphies seen in *Teleocrater* and later forms (Nesbitt, 2011; Nesbitt et al., 2017): its cervical vertebrae are not elongate, nor are they parallelogram-shaped, and so it did not have the long neck characteristic of that clade, and the vertebrae lack the hyposphene-hypantrum articulation. *Aenigmaspina* also lacks apomorphies of Aphanosauria, notably the blade-like dorsal end of the cervical neural spines, probable absence of osteoderms, divided parapophysis of the posterior cervical vertebrae, elongated deltopectoral crest of the humerus greater than 30% the length of the shaft, and wide distal end of the humerus greater than 30% of humerus length (Nesbitt et al., 2017).

A key character in *Aenigmaspina*, both the scanned core material and some of the additional specimens, is the presence of spine tables in the cervical and anterior dorsal vertebrae (Figs. 3A, C, D, F, H, I, 9B, C, D), which is an apomorphy of Crurotarsi (= Pseudosuchia; character 85 of Brusatte et al., 2010; character 191 of Nesbitt, 2011; character 321 of Ezcurra, 2016). A further crurotarsan apomorphy may be the short cervical ribs, no more than the length of two cervical centra (character 196 of Nesbitt, 2011). Other crurotarsan apomorphies cannot be established in the absence of skull and hind limb material. The absence of a number of characters of the vertebrae, such as hyposphene-hypantrum accessory articulations and any pneumatic features, confirms that *Aenigmaspina* is not an avemetatarsalian, an ornithodiran, or a dinosaur.

For the cladistic analysis, we first used the data matrix of 103 archosauromorph taxa and 600 characters of Ezcurra (2016). In fact, *Aenigmaspina* could be coded for 96 of the 600 characters (Appendix 2). We defined the ingroup as Archosauria and so deleted 73 archosauromorphs and basal archosauriforms, and we were left with 30 taxa and 401 informative characters. The analysis, perhaps surprisingly, yielded a single tree (Fig. 13A) in which *Aenigmaspina* is resolved as an ornithosuchid, paired with *Riojasuchus*, and then *Ornithosuchus*. Characters in support of Ornithosuchidae and the *Riojasuchus*-*Aenigmaspina* pairing are mainly uncoded in the latter but include sculpture on cranial bones and loss of sculpture on osteoderms, characters that frequently reverse across the cladogram. In fact, these relationships, and most others, collapse within two or three steps (Bremer support values of 2 or 3); the only robust nodes are the pairings of *Garjainia* and *Erythrosuchus*, and the clade of archosauriforms more derived than *Proterosuchus* (Bremer values >10).

For the second series of cladistic runs, we used the data matrix of 103 archosauromorph taxa and 676 characters of Ezcurra et al. (2017). *Aenigmaspina* could be coded for 104 of the 676 characters, comprising the 96 codings from the older data matrix plus eight more (Appendix 2). After deleting 74 archosauromorphs and basal archosauriforms, so that we could focus on Archosauria as the ingroup, we were left with 44 taxa and 447 informative characters, and the analysis yielded multiple trees, so we calculated strict and majority-rule consensus trees (Fig. 13B, C). These, perhaps bizarrely, place *Aenigmaspina* within Proterochampsia, paired with a clade comprising *Rhadinosuchus*, *Jaxtasuchus*, and *Doswellia*, occurring in all trees, but with low bootstrap value. The instability of this result is confirmed when we deleted three poorly coded taxa (*Nundasuchus*, *Erpetosuchus* sp., and *Archeopelta*) and achieved a single tree resolution (Fig. 13D) in which *Aenigmaspina* is still paired with *Rhadinosuchus*, but this clade is separated from the other proterochampsians and now paired with Ornithosuchidae. However, all those relationships have Bremer support values of only 1 or 2 and so can be broken with minimal perturbation. Shared characters, as with the pairing with Ornithosuchidae, concern osteoderms and sculpture and so are not unique.

Could *Aenigmaspina* be a proterochampsian? The parietal, if a part of the new archosaur, is flat and deeply sculptured, as in proterochampsians and *Doswellia* (Nesbitt, 2011). However, proterochampsians have a sharp oblique ridge across the lateral face of the

jugal (Nesbitt, 2011), which is not seen in the putative jugal here (Fig. 11E, F). Further, proterochampsians lack spine tables, a key feature of *Aenigmaspina*, and their osteoderms are sculptured and sometimes very thick (character 592 of Ezcurra, 2016).

Position of *Aenigmaspina* within Crurotarsi

Our cladistic analyses were not conclusive. We retain *Aenigmaspina* within Crurotarsi because of its unequivocal possession of spine tables, and despite the odd result placing it in Proterochampsia. It is hard to place *Aenigmaspina* within Crurotarsi, however. It appears to lack a well-rimmed lateral fossa on the centrum below the neurocentral suture in the dorsal vertebrae (character 354 of Ezcurra, 2016), an apomorphy of Suchia. Further, the shape of the osteoderms, which are anteroposteriorly longer than mediolaterally wide, is a character shared by many ‘rauisuchians’ and basal crocodylomorphs (character 407, state 1, of Nesbitt, 2011), but equally aetosaurs and other basal crocodylomorphs show osteoderms that are wider than long (state 2). If the parietal (Fig. 11G, H) belongs to *Aenigmaspina*, it is unfused and flat, lacking the midline ‘sagittal crest’ seen in *Erpetosuchus* as well as some ‘rauisuchians’ (character 59 of Nesbitt, 2011). Further, the flat area of the parietal is deeply sculptured with pits and ridges, as in phytosaurs, some crocodyliforms (*Protosuchus*, *Gracilisuchus*), proterochampsians, and *Doswellia* (Nesbitt, 2011), as well as in the erpetosuchid *Tarjadia* (Ezcurra et al., 2017:fig. 2).

The elongate scapula, at more than three times distal width, would have been regarded as an apomorphy of Theropoda (Serenó, 1999), but this is variable in basal dinosaurs (character 218 of Nesbitt, 2011), and in fact long, slender-bladed scapulae are known in small crurotarsans too, such as *Erpetosuchus* (Benton and Walker, 2002), *Tarjadia* (Ezcurra et al., 2017), and *Terrestriusuchus* (Crush, 1984).

We can eliminate most crurotarsan clades as homes for *Aenigmaspina*. First are the Phytosauria, which can be ruled out for *Aenigmaspina*, even though we lack key elements that might provide diagnostic characters, including primarily the skull (particularly the maxilla), the coracoid, the humerus, and the fibula. For one apomorphy (character 589 of Ezcurra, 2016), we can confidently say that the osteoderms lack sculpture on the external surface (Fig. 7). The isolated humeri of *Aenigmaspina* all appear to lack the ectepicondylar flange, an apomorphy of Phytosauria (Nesbitt, 2011). In addition, *Aenigmaspina* lacks some general, non-apomorphic characters of phytosaurs, such as cervical vertebrae with narrow neural canals, less than one-third the width of the centrum, amphicoelous centrum, parapophyses as hollows not projections, and diapophyses on long rods that extend from the lateral wall of the neural arch (Lucas et al., 2002). Further evidence that *Aenigmaspina* is not a phytosaur is that their teeth and massive, armored skull bones are commonly preserved, and yet not found at Pant-y-ffynnon, although their teeth have been found in other fissure localities such as Tytherington and Durdham Down (Benton et al., 2000).

We can also eliminate Aetosauria (= Stagonolepididae) as a potential inclusive clade for *Aenigmaspina*. The osteoderms of aetosaurs are diagnostic of genera, and they are the most common elements discovered (Nesbitt, 2011; Desojo et al., 2013). Aetosaur osteoderms have a characteristic rectangular shape, and they are generally mediolaterally wider than they are anteroposteriorly long (character 407 of Nesbitt, 2011; character 595 of Ezcurra, 2016). Further, they carry regular sculpturing of grooves and pits not seen in the osteoderms of *Aenigmaspina*, and the scapula and limb bones are far more slender than in the quadrupedal aetosaurs.

‘Rauisuchia’ is a paraphyletic group that includes multiple clades of large carnivores, some bipedal and some quadrupedal (Brusatte et al., 2010; Nesbitt et al., 2013). Key apomorphies of

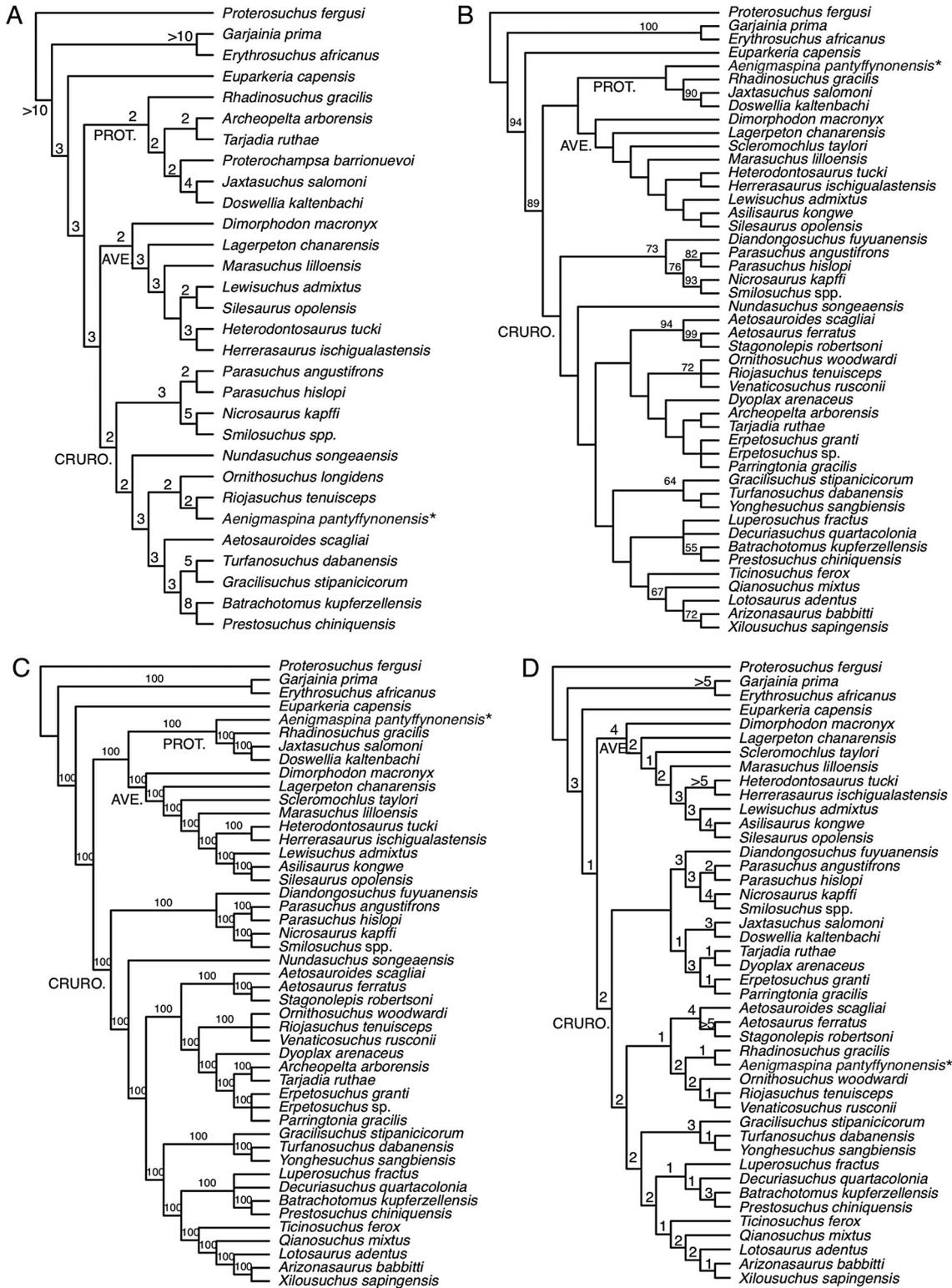


FIGURE 13. Phylogenetic analyses of *Aenigmaspina pantyffynonensis*, showing various resolutions, as **A**, an ornithosuchid, **B**, **C**, a proterochampsian, and **D**, a derived crurotarsan close to ornithosuchids. **A**, results of analysis based on the data matrix of Ezcurra (2016), and with non-archosaurs deleted: one tree of 1,256 steps, consistency index (CI) = 0.4682, retention index (RI) = 0.5508, and rescaled consistency index (RC) = 0.2578. **B–D**, results of analyses based on the data matrix of Ezcurra et al. (2017), with 76 additional characters and additional erpetosuchid taxa. **B**, **C**, results after deletion of 71 basal taxa and 228 uninformative characters: **B**, strict and **C**, majority-rule consensus trees from 18 trees, each of 1,643 steps, CI = 0.3938, RI = 0.5419, and RC = 0.2134. **D**, results following deletion of three further taxa (*Archeopelta arborensis*, *Nundasuchus songeaensis*, and *Erpetosuchus sp.*): a single tree is found with a tree length of 1,614 steps, CI = 0.3990, homoplasy index (HI) = 0.6462, RI = 0.5396, and RC = 0.2153. Numbers in **A** and **D** are Bremer support values, in **B** bootstrap values (>50%), and in **C** nodes occurring in all source trees are indicated by 100 (%). **Abbreviations:** AVE., Avemetatarsalia; CRURO., Crurotarsi; PROT., Proterochampsia.

‘rauisuchian’ clades are in the skull and so cannot be coded for *Aenigmaspina*, and yet their large, recurved teeth are often found isolated. We suggest that *Aenigmaspina* cannot be a ‘rauisuchian’ because it lacks any diagnostic characters of the included clades, isolated ‘rauisuchian’ teeth do not occur, and it is far too small and slender. *Aenigmaspina* cannot have been more than 1 m in length, whereas ‘rauisuchians’ are generally (but not always) much larger (Nesbitt et al., 2013).

Apomorphies for Crocodylomorpha are in the skull, the clavicles (specifically their absence), the coracoid, the humerus, the carpals, and the ilium (Nesbitt, 2011), but we can probably exclude *Aenigmaspina* from this clade, because no crocodylomorph has such expanded ‘V’- or ‘Y’-shaped spine tables, generally just a modest expansion of the distal neural spine.

Three crurotarsan clades might include *Aenigmaspina*: Ornithosuchidae, Erpetosuchidae, and Gracilisuchidae. Ornithosuchidae has apomorphic characters in the skull, the cervical and sacral vertebrae, the humerus, the pelvic girdle, the femur, the astragalus-calcaneum, and the metatarsal V (Nesbitt, 2011; Ezcurra, 2016). *Aenigmaspina* lacks one ornithosuchid apomorphy: the cervical vertebrae showing the middle portion of the ventral keel extending ventral to the centrum rims (character 190 of Nesbitt, 2011). The keels on the cervicals of *Aenigmaspina* are fully dorsal (Fig. 3A–E). Further, as with the other crurotarsan clades thus far considered, ornithosuchids are generally much larger animals than *Aenigmaspina*.

The Erpetosuchidae is another crurotarsan clade that has been identified based on new studies of the taxa *Erpetosuchus*, *Parringtonia*, and *Tarjadia* and found not to lie close to the origin of crocodylomorphs, as had once been thought (Olsen et al., 2000; Benton and Walker, 2002), but perhaps close to ornithosuchids and aetosaurs (Ezcurra et al., 2017). The diagnostic characters of *Erpetosuchus* itself are largely in the skull, but there are differences in the vertebrae. *Erpetosuchus* possesses anteroposteriorly narrow neural spines in more anterior vertebrae. Furthermore, although these display spine tables on the neural spines, they are ‘T’-shaped rather than ‘Y’-shaped as in *Aenigmaspina*. In addition, the osteoderms of *Erpetosuchus* are ornamented (Benton and Walker, 2002), whereas those of *Aenigmaspina* are smooth. These characters, although not apomorphies, exclude *Aenigmaspina* from *Erpetosuchus*. A second erpetosuchid, *Parringtonia*, also has deeply sculptured, square-shaped osteoderms, and a scapula with broader proximal end and the glenoid more offset from the blade, but the dorsal vertebrae are similar, and especially with a branching, slightly ‘Y’-shaped spine table (Nesbitt and Butler, 2012). A third erpetosuchid, *Tarjadia*, originally described as an archosaur of uncertain phylogenetic position (Arcucci and Marsicano, 1998), shows much more information from new material (Ezcurra et al., 2017). It differs from *Aenigmaspina* in having nearly flat-topped spine tables on the presacral vertebrae, with multiple rows (four) of osteoderms, square paramedian osteoderms and semicircular lateral osteoderms, all of them thick and bearing a pitted sculpture of circular depressions. Ezcurra et al. (2017:1479) identified the character “vertebral spine tables with a concave dorsal surface” as an apomorphy of Erpetosuchidae, but the concavity of the dorsal surface of the spine table corresponds to an angle of about 5° for each lateral portion, as compared with 45° in *Aenigmaspina*, where the concavity makes the dorsal end of the neural spine distinctly ‘Y’-shaped when viewed anteriorly or posteriorly (Fig. 3A, C, F, H).

The gracilisuchids are a further clade of derived small crurotarsan archosaurs, diagnosed by characters of the premaxilla, maxilla, nasal, frontal, calcaneum, and osteoderms (Butler et al., 2014). Of these, only the osteoderm character can be determined in *Aenigmaspina*, and it lacks the characteristic longitudinal bend near the lateral edge seen in presacral paramedian scutes. Indeed, the osteoderms of gracilisuchids are asymmetric, and they are paired, not apparently fused as in *Aenigmaspina*. A further apomorphy

of Gracilisuchidae, the fan-shaped neural spine of cervical and dorsal vertebrae in the shape of a trapezoid (character 363 of Ezcurra, 2016), is also absent; *Aenigmaspina*’s neural spines are subrectangular (Figs. 3, 4, 9). *Gracilisuchus* also has a circular depression in the mid-dorsal region of the neural arch on the cervical vertebrae, and its osteoderms have a longitudinal keel on the dorsal surface, not ventral as in *Aenigmaspina*, and the keel differs in its mediolateral position (Lecuona et al., 2017).

CONCLUSION

Aenigmaspina is an archosaur and a crurotarsan, but not a phytosaur, aetosaur, ‘rauisuchian,’ or crocodylomorph; it might be an ornithosuchid, erpetosuchid, or gracilisuchid. It shares the ‘Y’-shaped spine tables in cervical and dorsal vertebrae with erpetosuchids, but the spine table in *Aenigmaspina* is much more deeply angled, and the osteoderms are very different in shape, organization, and sculpture. Even so, we find that *Aenigmaspina* is a previously unnamed form, and so we erect the new genus and species *Aenigmaspina pantyffynnonensis* so that it can be compared with other new archosaur finds for eventual resolution of its phylogenetic relationships through recovery of more fossil material.

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DATA ARCHIVING STATEMENT

The CT scan is the property of the NHMUK and may be accessed with a reasonable request by contacting the Palaeontology Section, Earth Science Department, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

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