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## BRAINCASE OF *PANPHAGIA PROTOS* (DINOSAURIA, SAUROPODOMORPHA)

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**ABSTRACT**—We describe a partial braincase of the basal sauropodomorph *Panphagia protos* from the Upper Triassic (mid-Carnian) horizons of the Ischigualasto Formation. The disarticulated braincase from a subadult individual includes one frontal, both parietals, one prootic, and the supraoccipital. The frontal is longer anteroposteriorly than it is wide transversely, has a small anterolateral process, and an elongate oval depression for the olfactory bulb. The supraoccipital is broader transversely than it is deep dorsoventrally and lacks a pronounced median nuchal eminence. Some braincase features that characterize more derived basal sauropodomorphs are not present in *Panphagia*, including a broader frontal and reduced anterior tympanic and floccular recesses. *Panphagia* appears to represent an early stage in the evolution of sauropodomorph dinosaurs.

**RESUMEN**—Describimos la caja craneana parcial del sauropodomorfo basal *Panphagia protos* proveniente de horizontes del Triásico superior (Carniano medio) de la Formación Ischigualasto. La caja craneana desarticulada es de un individuo sub-adulto e incluye un frontal, dos parietales, un proótico y el supraoccipital. El frontal es más largo anteroposteriormente que ancho transversalmente, tiene un pequeño proceso anterolateral y una depresión alargada oval para el bulbo olfatorio. El supraoccipital es transversalmente más ancho que dorsoventralmente alto y carece de una eminencia nuchal media pronunciada. Algunas de las características que caracterizan los neurocráneos de sauropodomorfos basales más derivados no están presentes en *Panphagia*, incluyendo el frontal ancho y la reducción de las cavidades timpánica anterior y floccular. *Panphagia* parece representar una etapa temprana en la evolución de los dinosaurios sauropodomorfos.

### INTRODUCTION

The earliest and most basal sauropodomorphs now include taxa known from relatively complete skeletons, such as *Eoraptor* (Serenó et al., 1993, 2013; Martínez et al., 2011), *Panphagia* (Martínez and Alcober, 2009), *Saturnalia* (Langer et al., 1999, 2007; Langer, 2003), and *Pampadromaeus* (Cabeira et al., 2011). Taken together, these genera document well the external morphology of the skull and postcranial skeleton. What is conspicuously absent in this material, however, is detailed information on the braincase. Only a few isolated elements of the braincase have been found in *Eoraptor* (Serenó et al., 2013) and *Panphagia* (Martínez and Alcober, 2009), and these have not yet been described in detail.

Discovered in 2006 in the mid-Carnian horizons of the Ischigualasto Formation, the basal sauropodomorph *Panphagia protos* is known from a single specimen that preserves several disarticulated cranial elements that include portions of the braincase (PVSJ 874; Martínez and Alcober, 2009). These bones are well preserved and include the frontal, parietal, supraoccipital, and prootic. We describe these bones in detail below and compare them with other basal dinosaurs and more advanced sauropodomorphs.

The braincase anatomy is well documented in several basal sauropodomorph genera of Late Triassic (post-Carnian) or Early Jurassic age, including *Thecodontosaurus* (YPM 2192), *Efraasia*, *Plateosaurus*, *Massospondylus*, *Anchisaurus*, and *Melanorosaurus* (Galton, 1984, 1985; Kermack, 1984; Galton and Bakker, 1985; Gow, 1990; Benton et al., 2000; Sues et al., 2004; Yates, 2003, 2004, 2007; Fedak and Galton, 2007). Comparative information on the braincase in the earliest and most basal theropods, by contrast, is poorly known. In the well-preserved skull of *Herrerasaurus*, the neurocranial elements are obscured laterally, dorsally, and anteriorly by dermal bones of the skull roof (Serenó

et al., 1993; Sereno and Novas, 1994), and computed tomographic scans of the specimen failed to resolve significant internal detail. The braincase is not known in other herrerasaurids, including *Staurikosaurus* (Colbert, 1970; Bittencourt and Kellner, 2009), *Chindesaurus* (Long and Murry, 1995), and *Sanjuansaurus* (Alcober and Martínez, 2010). In the contemporaneous (mid-Carnian) theropod *Eodromaeus* (Martínez et al., 2011) and somewhat younger (Norian) *Tawa* (Nesbitt et al., 2009), more of the braincase is preserved and exposed but has yet to be described. Comparative information on the braincase of basal ornithischians is fairly limited as well. Despite excellent preservation of the skull in the basal ornithischians *Lesothosaurus* and *Heterodontosaurus*, the braincase is poorly exposed and has not been described from computed tomographic imaging (Serenó, 1991, 2012; Norman et al., 2011). The braincase of *Lesothosaurus* is the better known of these two ornithischians and has been figured in lateral view with sutures indicated (Serenó, 1991:fig. 13A, B). The sidewall of the braincase in *Heterodontosaurus* is not exposed, and reconstructions of it do not indicate sutures (Norman et al., 2011:fig. 15). Immediate dinosaur outgroups, such as the silesaurids, also lack detailed comparative information on the braincase. Although the disarticulated braincase in *Silesaurus* has been reconstructed in multiple views, there is little accompanying descriptive information and no way to discern preserved from reconstructed morphology (Dzik, 2003:fig. 7). The external and internal morphology of braincase have not been described.

In sum, an outline of braincase evolution in basal sauropodomorphs and in basal dinosaurs in general has yet to be formulated. At present, we cannot recognize with confidence primitive versus derived conditions in the neurocranium at various levels within Dinosauria. We work toward that goal with the detailed documentation of portions of the braincase in the basal sauropodomorph *Panphagia*. Braincase characters have been incorporated into basal sauropodomorph phylogenies (e.g., Yates, 2003, 2004, 2007) and are likely to garner an increasing presence in future datasets.

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## MATERIALS AND METHODS

## Materials

Skull bones studied include the left frontal, both parietals, right prootic, and supraoccipital of the holotype of *Panphagia protos* (PVSJ 874). These disarticulated bones are fully prepared and exposed in all views.

## Orientation and Terminology

Because the bones were found in isolation, we assumed an orientation in our figures consistent with that in the intact braincases of closely related taxa (e.g., *Adeopapposaurus*; Martínez, 2009). We employed traditional, or ‘Romerian,’ directional terms over veterinarian alternatives (Wilson, 2006). ‘Anterior’ and ‘posterior’ are employed rather than ‘rostral,’ ‘cranial,’ or ‘caudal.’ When vernacular terms in English were not available or widely used, we employed appropriate anatomical terms from the *Nomina Anatomica Avium* (Baumel et al., 1993).

We followed the phylogenetic definitions proposed by Sereno (2005). Sauropodomorpha, for example, in this work is regarded as a stem-based taxon defined as the most inclusive clade containing *Saltasaurus loricatus* but not *Passer domesticus* or *Triceratops horridus*. With this formulation, the definition does not depend on the monophyly of other suprageneric taxa (e.g., Saurischia, Prosauropoda).

**Institutional Abbreviations**—PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; YPM, Yale Peabody Museum, Yale University, New Haven, Connecticut, U.S.A.

## DESCRIPTION

## Skull Roof

**Frontal**—The frontal is anteroposteriorly longer than it is transversely broad (Fig. 1). Its maximum length is greater than twice its maximum width across the posterolateral processes, and the posterior end is transversely wider than the anterior end (Fig. 1A, B). The transversely broad sutural surface for the nasal faces dorsally and is located medial to the sutural surface for the prefrontal. These nasal and prefrontal lay adjacent to one another on the frontal, although a short anterior process of the frontal separates them (Fig. 2A). Although the medial portion of the anterior end of the frontal is broken away, it appears to have extended to a point along the midline.

The sutural surface for the prefrontal, which is exposed in dorsal and lateral views, is transversely narrow (Fig. 1A, C). In dorsal view, the articular surface for the prefrontal is well marked both anteriorly and posteriorly, the posterior tip of which lies along the orbital rim rather than on the dorsal surface of the frontal (Fig. 1A).

Most of the medial edge of the frontal forms a straight, vertical margin for its opposite (Fig. 1A, B), although there is a shallow medial sulcus bounded ventrally by a short shelf (Fig. 1D). More posteriorly, the medial edge is convex and then curves slightly away from the midline (Fig. 1A, B), which appears to be a natural asymmetry between left and right frontals. The portion of the orbital border formed by the frontal is proportionally long, forming just over 50% of the total length of the bone (Fig. 1A).

A ‘V’-shaped notch for articulation with the postorbital and the arcuate rim of the supratemporal fossa are sharply defined (Fig. 1A). Medial to the slot articulation for the postorbital and within the supratemporal fossa, a subtriangular process projects posterolaterally (Fig. 1A). This tip of this process likely marks the sutural triple junction between the frontal, postorbital, and pari-

etal (Fig. 2A). The posterior edge of the frontal is marked by sutural contact with other bones and likely contributed little if any to the anterior margin of the supratemporal fenestra (Fig. 2A). The posterior edge of the frontal is arcuate in dorsal view, curving anterolaterally rather than following a transverse course (Fig. 3).

The ventral surface of the frontal has two distinct surfaces separated by a medially convex ridge, or crista cranii (Fig. 1B). In *Panphagia*, the crista cranii is developed as a pair of parallel ridges rather than a single ridge (Figs. 1B, 3A), as occurs in at least in the posterior part of the crista cranii in *Pantydraco* (Galton and Kermack, 2010:fig. 4D; Fig. 3B). The surface between these ridges is flat along the anterior one-third of its extension and slightly concave in its posterior two-thirds in *Panphagia*.

The orbital roof is relatively narrow transversely, expanding in width slightly posteriorly. The rim of the orbit is gently upturned, and the orbital surface faces ventrolaterally (Fig. 1C, D). The surface medial to the crista cranii is transversely concave and forms part of the roof of the nasal cavity (cavum nasi; Baumel and Witmer, 1993). An elongate oval fossa accommodated the olfactory bulb (Figs. 1B, 3A). Medial to this fossa, a longitudinal trough may have housed the olfactory nerve (Fig. 1B) as proposed previously in *Coelophysis* (Raath, 1977:fig. 5F). A ridge continues anteriorly and may have supported cartilage of the nasal cavity, judging from hypothesized conchal homologies (Witmer, 1995a) and the condition in the squamate *Ctenosaura* (Oelrich, 1956).

Anterolateral to the fossa for the olfactory bulb, another depression is present and may represent a portion of the roof of the cavum nasi (Fig. 3A; *Majungasaurus*, *Tyrannosaurus*; Witmer and Ridgely, 2008:figs. 5A, 6A, E, G). Surfaces medial and lateral to the ridge likely represent parts of the roof of the cavum nasi. The olfactory nerve may have reached the olfactory bulb more laterally than hypothesized for *Coelophysis* (Raath, 1977:fig. 21), either on the anterolateral aspect of the bulb as in *Tyrannosaurus* (Witmer and Ridgely, 2008:fig. 6B) or more laterally as in crocodylians (Shiino, 1914).

The posterior expansion of the frontal presents a shallow fossa cranii anterioris (sensu Baumel and Witmer, 1993; Fig. 1B) for the telencephalon, which occupies the entire width of the frontal endocranial surface (Fig. 3A). The endocranial surface represents half the width of the frontal at the posterior end of the bone.

The sutural area for the laterosphenoid is not well defined (Fig. 1B). A small, anteroposteriorly elongated depression is present medial to the posterior end of the crista cranii, which may represent an articular surface for the head of the laterosphenoid. The orbitosphenoid-frontal contact has been suggested in this location in *Plateosaurus* (Galton, 1984), although in specimens of *Massospondylus* (Gow, 1990:fig. 3A) and *Allosaurus* (McClelland, 1990:fig. 11) the orbitosphenoid does not contact the frontal.

The relatively long proportions of the frontal of *Panphagia*, in which its maximum length is greater than two times the maximum width at the posterolateral process (Figs. 1A, B, 2A), are similar to those found in *Silesaurus* (Dzik, 2003:fig. 6D), *Eoraptor* (PVSJ 512), *Pantydraco* (Yates, 2003:fig. 4A), and *Coelophysis* (Raath, 1977:figs. 3B, 5F) and differ from the relatively wider frontals of *Lesothosaurus* (Sereno, 1991:figs. 11B, 12B), *Herrerasaurus* (Sereno and Novas, 1994:figs. 1C, 7B, 8B; Fig. 2B), and many basal sauropodomorphs (Fig. 2C, D). The proportionally long orbital border formed by the frontal is similar to that in *Herrerasaurus* (Fig. 2B), *Coelophysis* (Raath, 1977:fig. 5B, F), *Silesaurus* (Dzik, 2003:fig. 6D), and some basal sauropodomorphs (Fig. 2D; also *Pantydraco*, Kermack, 1984:fig. 4; Galton and Kermack, 2010:fig. 4A–C; *Massospondylus*, Yates, 2003:fig. 2C, 4A; Sues et al., 2004:fig. 3A). The frontal contribution to the orbital border is proportionately shorter in *Lesothosaurus*

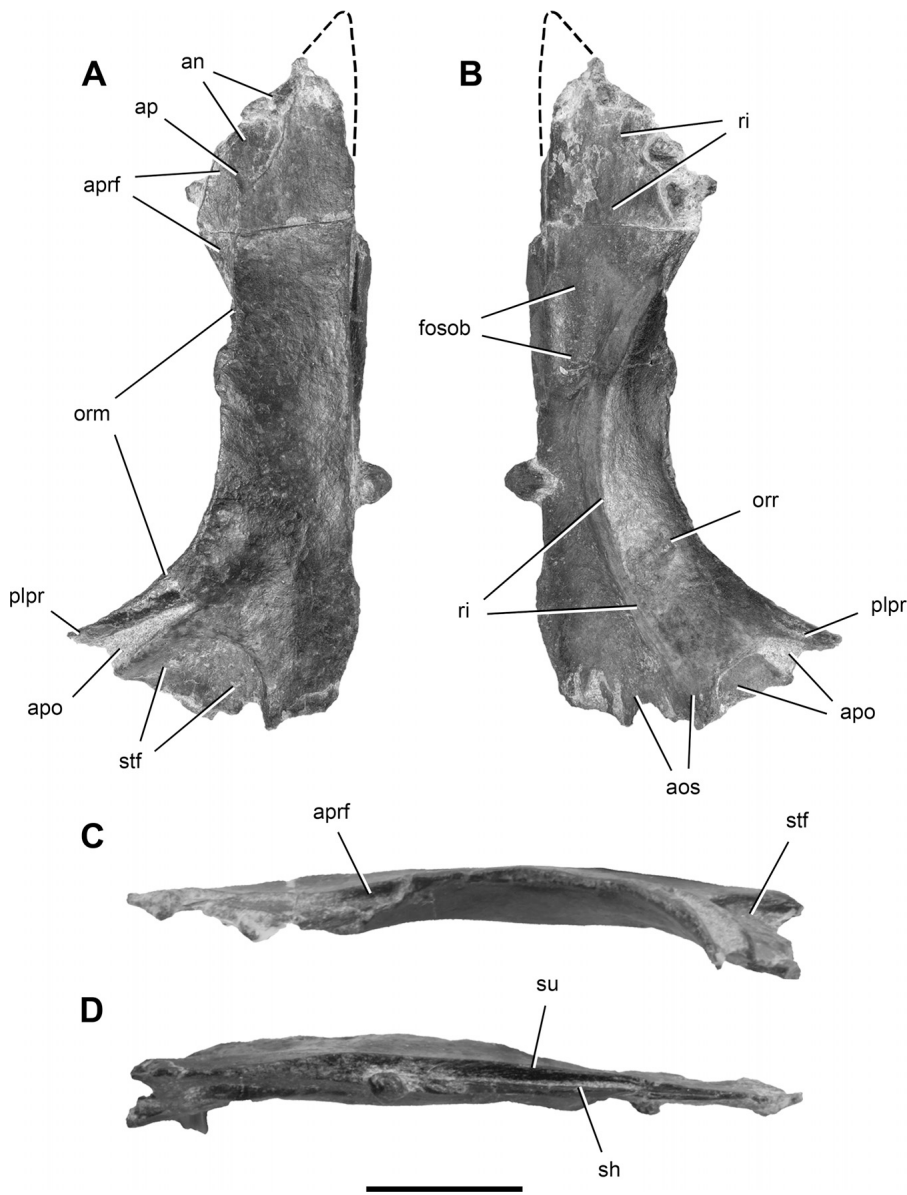


FIGURE 1. Left frontal of *Panphagia protos* (PVSJ 874) in dorsal (A), ventral (B), lateral (C), and medial (D) views. **Abbreviations:** **an**, articular surface for the nasal; **aos**, articular surface for the orbitosphenoid; **ap**, anterior process; **apo**, articular surface for the postorbital; **aprf**, articular surface for the prefrontal; **fosob**, fossa for the olfactory bulb; **orm**, orbital margin; **orr**, orbital roof; **plpr**, posterolateral process; **ri**, ridge; **sh**, shelf; **stf**, supratemporal fossa; **su**, sulcus. Scale bar equals 1 cm.

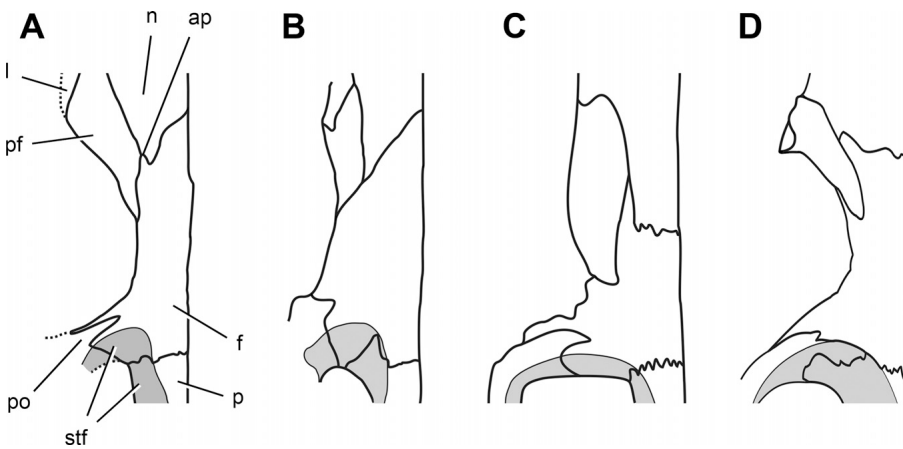


FIGURE 2. Dorsal view of partial skull roof of the basal dinosaurs *Panphagia* (A), *Herrerasaurus* (B), *Plateosaurus* (C), and *Adeopapposaurus* (D). The supratemporal fossa is shaded gray. Modified from Sereno and Novas, 1994 (B); Galton, 1984 (C); and Martínez, 2009 (D). **Abbreviations:** **ap**, anterior process; **f**, frontal; **l**, lacrimal; **n**, nasal; **p**, parietal; **pf**, prefrontal; **po**, postorbital; **stf**, supratemporal fossa. The drawings are not in the same scale.

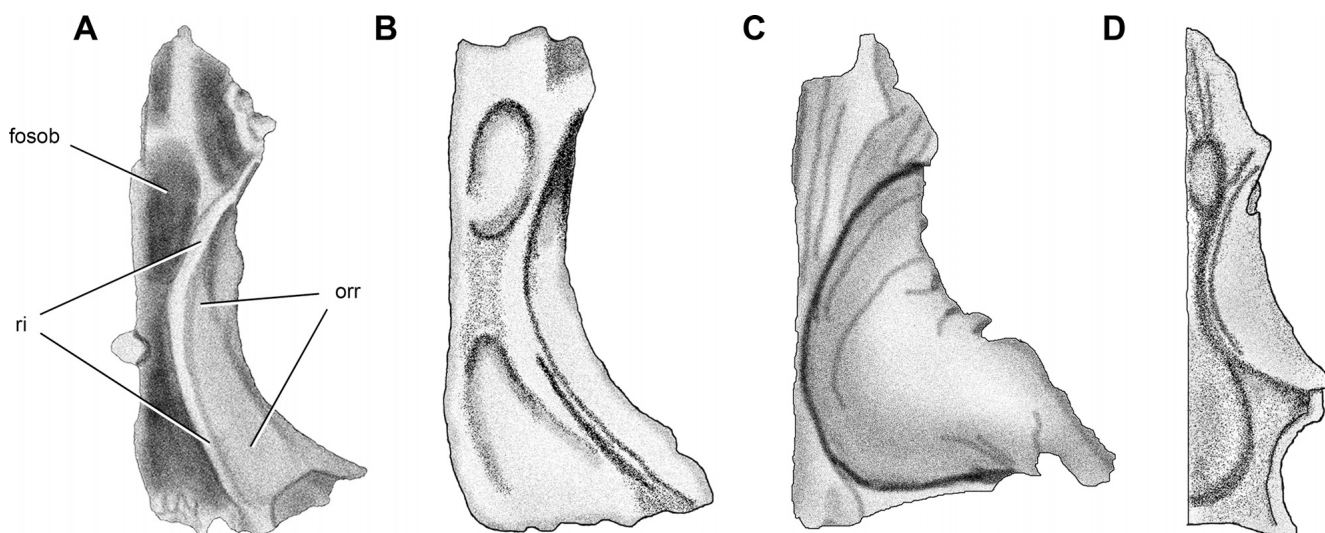


FIGURE 3. Ventral view of the frontal of the basal dinosaurs *Panphagia* (A), *Pantydraco* (B), *Plateosaurus* (C), and *Coelophysis* (D). Modified from Galton and Kermack, 2010 (B); Galton, 1984 (C); and Raath, 1977 (D). **Abbreviations:** fosob, fossa for the olfactory bulb; orr, orbital roof; ri, ridge. The drawings are not in the same scale.

(Serenó, 1991:fig. 11B) and other basal sauropodomorphs such as *Plateosaurus* (Fig. 2C), *Melanorosaurus* (Yates, 2007:figs. 3A, B, 7), and *Lufengosaurus* (Barrett et al., 2005:fig. 3A, B). The transversely narrow sutural surface for the prefrontal (Figs. 1A, C, 2A) is similar to that in *Pantydraco* (Galton and Kermack, 2010:fig. 4B) and narrower than that in *Melanorosaurus* (Yates, 2007:figs. 3A, B, 7), *Adeopapposaurus* (Fig. 2D), and *Riojasaurus* (PVSJ 849). The acute 'V'-shaped notch for articulation with the postorbital (Fig. 1A) is similar to that in *Eoraptor* (Langer, 2004), *Pantydraco* (Yates, 2003), *Plateosaurus* (Fig. 2C), and *Coelophysis* (Raath, 1977:fig. 5B). The articular notch is shorter in *Herrerasaurus* (Fig. 2B), is intermediate in length in *Lesothosaurus* (Serenó, 1991:fig. 11B), and is 'U'-shaped and broader in *Heterodontosaurus* (Norman et al., 2011:fig. 6A). The exclusion of the frontal from the margin of the supratemporal fenestra resembles the condition in *Herrerasaurus* (Fig. 2B), *Adeopapposaurus* (Fig. 2D), *Megapnosaurus kayentakatae* (Rowe, 1989:fig. 1C, D), and *Lesothosaurus* (Serenó, 1991:fig. 11B). In *Heterodontosaurus* (Norman et al., 2011:fig. 1A) and *Plateosaurus* (Fig. 2C), in contrast, the frontal has a concave posterior margin that contributes to the supratemporal fenestra.

**Parietal**—The parietal, which is best preserved on the left side (Fig. 4), forms a broad arch over the braincase. The posterolateral ramus extends posterolaterally as a thin lamina between the squamosal and paroccipital processes. In dorsal view, the medial half of the parietal is flat and relatively broad transversely. A low sinusoidal ridge forms the medial margin of the supratemporal fossa, which diverges anteriorly and joins the dorsal border of the posterolateral ramus posteriorly (Fig. 4A, C). The sutural surface for the postorbital anterolaterally has suffered some breakage and is not clearly preserved.

The anterior border of the main body of the parietal is convex, with the lateral extremity of the border more posteriorly set than its medial part. The medial one-half of this border is serrated, suggesting an interdigitating suture with the frontal. An articular depression for the frontal is present on the lateral one-half of the anterior margin. The base of the posterolateral ramus is triangular in cross-section, and the ramus is flattened distally and twists into a vertical plane (Fig. 4). The anterolat-

eral surface of the ramus has a depression dorsally limited by a ridge for articulation with the parietal process of the squamosal (Fig. 4F).

The posteromedial surface of the posterolateral ramus is dorsoventrally concave proximally and flattens distally (Fig. 4E). The posteroventral border of the ramus is developed into a convex prominence near its base, which forms the ventral border of the posteromedial concavity of the ramus (Fig. 4B, E). This prominence is dorsal to a foramen completed ventrally by a notch on the supraoccipital for the vena occipitalis externa (= caudal middle cerebral vein; sensu Witmer and Ridgely, 2008). A weakly differentiated anteroposteriorly short surface for articulation with the laterosphenoid is present ventrally at the anterolateral end of the parietal (Fig. 4B).

A deep 'C'-shaped sulcus that is convex posteriorly is present on the ventral surface of the parietal (Fig. 4B). It contacts the lateral border of the parietal and lies adjacent to a ventrolaterally facing notch (Fig. 4B). Medially, the 'C'-shaped sulcus approaches the midline and then turns anterolaterally, ending in a narrow and deep anteroposteriorly elongate fossa, which likely contacted the sinus occipitalis (Fig. 4B). A series of small grooves, presumably for smaller blood vessels, emerge from the anterior aspect of the elongate fossa. Additional very shallow vascular grooves are present on the ventral surface of the parietal. The 'C'-shaped sulcus is contacted on the posterior side of its lateral portion by a posterolaterally oriented short, wide, and shallow trough (Fig. 4B). This trough is located on the ventral surface of the prominence of the posteroventral border of the posterolateral ramus. In this depression fits a convex anterodorsolateral surface of the supraoccipital located immediately anterior to the notch for the vena occipitalis externa. If modeled on the encephalic venous system in modern birds (Baumel, 1993:figs. 12, 13B) and basal diapsids (O'Donoghue, 1920), the posterior part of the sinus petrosus caudalis was probably located within the short posterolateral trough formed by the parietal and supraoccipital. This sinus likely reached the 'C'-shaped sulcus anteriorly. At this point, it would have diverged along each branch of the 'C.' The medial branch probably ended in the sinus occipitalis. This sinus is interpreted here as the homologue of a more anterior section of the sinus

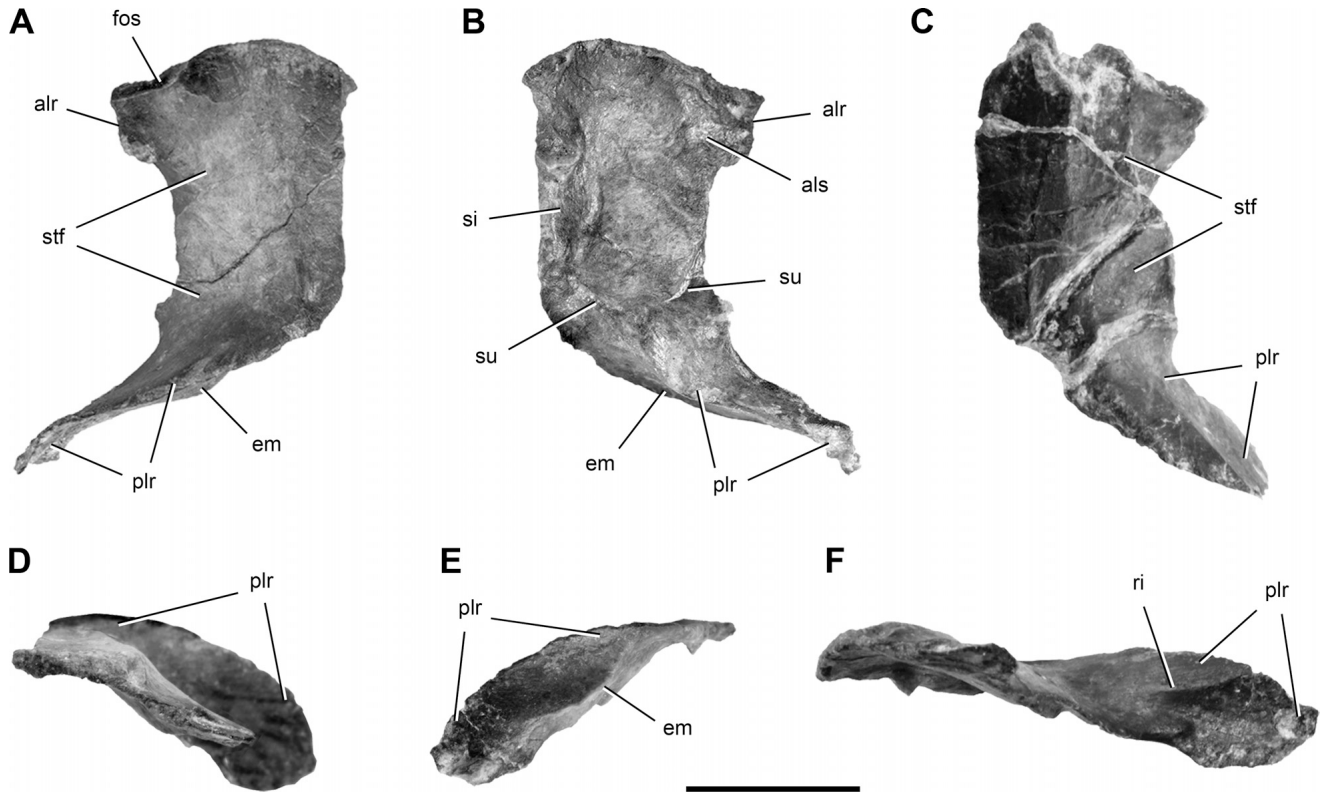


FIGURE 4. Left and right parietals of *Panphagia protos* (PVSJ 874). Left parietal in dorsal (A) and ventral (B) views. Right parietal in dorsal (C) view. Left parietal in anterior (D), posterior (E), and anterolateral (F) views. **Abbreviations:** *alr*, anterolateral ramus; *als*, articular surface for the laterosphenoid; *em*, eminence; *fos*, fossa; *plr*, posterolateral ramus; *ri*, ridge; *si*, sinus; *stf*, supratemporal fossa; *su*, sulcus. Scale bar equals 1 cm.

petrosus caudalis (Baumel, 1993:figs. 12, 13). The lateral branch would have exited the *cavum cranii* through the notch in the lateral border of the parietal and possibly one of the notches on the posterodorsal border of the prootic (see below). The parietal and supraoccipital are separated in the midline by a parietal fenestra.

Comparing the parietal of *Panphagia* in dorsal view with that in other basal dinosaurs, the medial margin of its supratemporal fossa diverges away from the midline anteriorly (Fig. 4A, C), as in *Herrerasaurus* (Serenó and Novas, 1994:figs. 4, 7B, 8B), *Eoraptor* (PVSJ 512), *Adeopapposaurus* (Martínez, 2009:figs. 2A, 3B, 5B), and *Plateosaurus* (Galton, 1984:fig. 3C). This differs from the parasagittal orientation in the basal theropods *Coelophysis* (Raath, 1977:fig. 5B) and *Megapnosaurus kayentakatae* (Tykoski, 1998:figs. 3, 5). The sinus connecting the posterior petrosal sinus and extracranial space is clearly present among non-avian reptiles (as the ‘vena parietalis’; Bruner, 1907; O’Donoghue, 1920; Romer, 1956). Osteological correlates of this sinus have been identified in dinosaurs (Galton, 1989; Galton and Kermack, 2010), including *Archaeopteryx* (Domínguez Alonso et al., 2004), but it has not been reported in Recent birds (e.g., Pearson, 1972; Baumel, 1993; Seldmayr, 2002). The parietal and supraoccipital are separated in the midline by a postparietal fenestra, as in *Eoraptor* and in most basal sauropodomorphs (e.g., *Melanorosaurus*, Yates, 2007; *Coloradisaurus*, Bonaparte, 1978; *Anchisaurus*, *Plateosaurus*, *Massospondylus*, and *Adeopapposaurus*, Martínez, 2009:fig. 3B; *Riojasaurus*, Bonaparte and Pumares, 1995; *Sarahasaurus*, Rowe et al., 2010; *Mussaurus*, Pol and Powell, 2007). There is no dorsal opening between these bones in the basal neotheropods *Megapnosaurus kayentakatae* (Tykoski,

1998:figs. 3, 5) and *Majungasaurus* (Sampson and Witmer, 2007) or in the ornithischian *Heterodontosaurus* (Norman et al., 2011).

### Braincase

**Supraoccipital**—We describe the supraoccipital with its principal external surface facing posterodorsally (Figs. 5, 6, 7A), as it is positioned in an intact braincase of *Plateosaurus* (Galton, 1984). In posterior and posterodorsal views (Figs. 5A, 6A), the supraoccipital has an elliptical shape that is broader transversely than deep dorsoventrally, as in most basal sauropodomorphs. The dorsomedian or nuchal region of the supraoccipital between the notches of the vena occipitalis externa is shallow. There are no ventrolateral processes as occur in *Pantyraco* (Galton and Kermack, 2010), and the nuchal region is developed only as a low median eminence (Figs. 5A, C, 6A). Shallow fossae are present to either side of the median eminence (Fig. 6A). The notches for the vena occipitalis externa are not simple slots but rather have depth and a pocket-like form (Figs. 5E, 6A). The passage through the supraoccipital is oblique to the occipital surface (Figs. 5A, C, D, F, 6A), as apparently is also the case in a juvenile specimen of *Massospondylus* (Gow, 1990:fig. 6B). The posteroventral border of the supraoccipital exhibits five concavities; the medial one corresponds to a sharp edge that represents the dorsal border of the foramen magnum (Fig. 6A). The supraoccipital contribution to the foramen magnum is proportionally narrow compared with the rest of the ventral contour of the bone.

In posterodorsal view, the anterodorsal contour of the supraoccipital between the vena occipitalis externa notches is

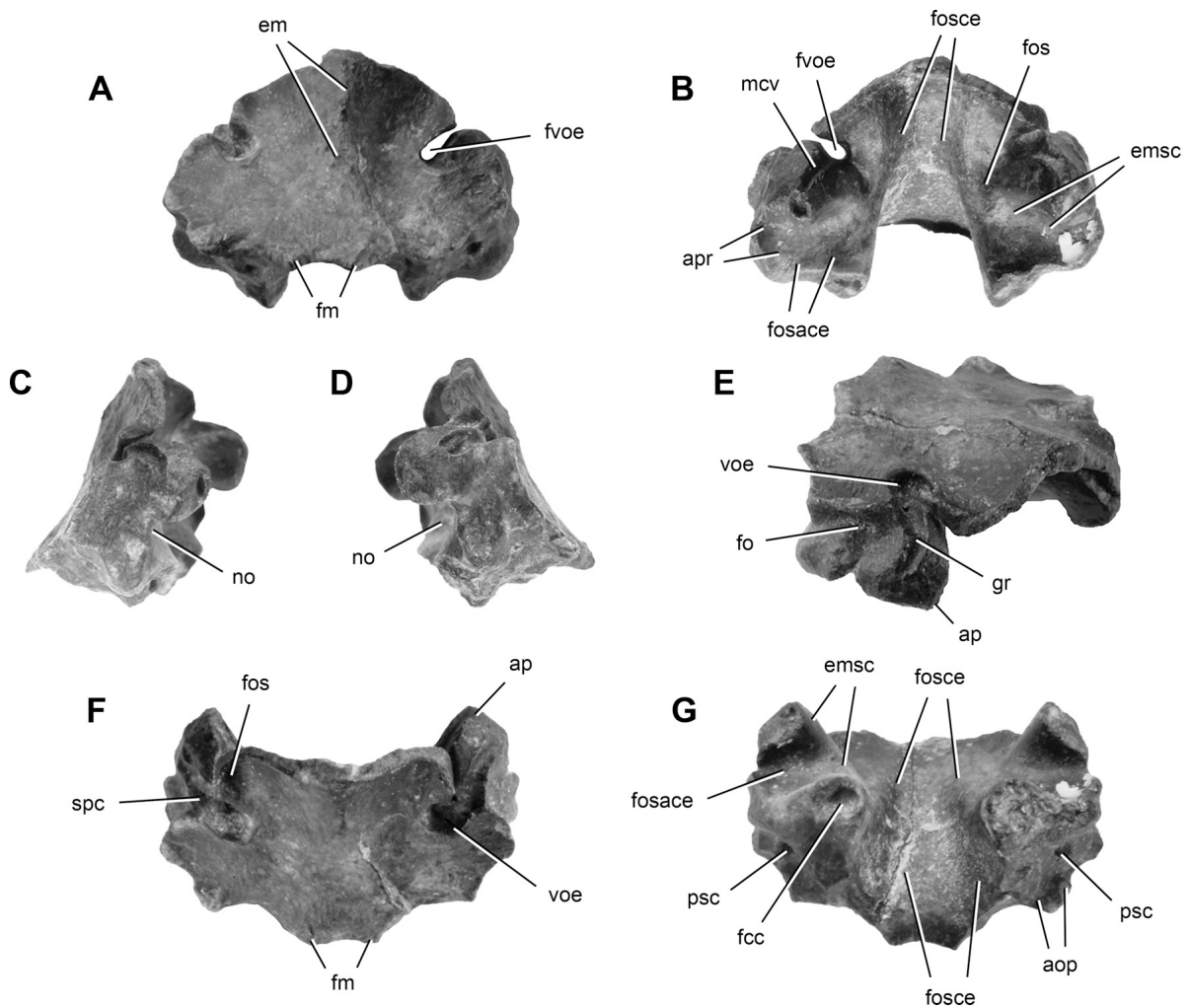


FIGURE 5. Supraoccipital of *Panphagia protos* (PVSJ 874) in posterior (A), anterior (B), right lateral (C), left lateral (D), posterodorsolateral (E), dorsal (F), and ventral (G) views. Anterior is towards the top of the page in F and G. **Abbreviations:** aop, articular surface for the exoccipital-opisthotic; ap, articular surface for the parietal; apr, articular surface for the prootic; em, eminence; emsc, eminentia canalis semicircularis; fcc, foramen crus commune; fm, foramen magnum; fo, foramen; fos, fossa; fosace, fossa auriculæ cerebelli; fosce, fossa cerebelli; fvoe, foramen for the vena occipitalis externa; gr, groove; mcv, medial cerebral vein; no, notch; psc, posterior semicircular canal; spc, sinus petrosus caudalis; voe, vena occipitalis externa. Scale bar equals 1 cm.

smoothly arched, with only a small median prominence (Figs. 5A, 6A). The lateral and posteroventral articular surfaces for the exoccipital-opisthotic are angled at nearly 90° in posterior view (Fig. 6A), in contrast to the straight posterodorsal border in *Lesothosaurus* (Thulborn, 1970:fig. 1D; Sereno, 1991:fig. 11C) and *Melanorosaurus* (Yates, 2007:figs. 4A, B, 8). The lateral margins of the supraoccipital are gently everted in posterior view (Fig. 5C–E, G).

A groove is present in the notch of the vena occipitalis externa (Fig. 5E), which turns sharply in the ventromedial region of the fossa, as has been described for *Massospondylus* (Gow, 1990). Both extremities of the groove are anterolaterally oriented and converge posteromedially in the deepest part of the notch, where they form the aforementioned sharp turn. The lateral-most part of the groove (Fig. 5C, E) may represent the homologue of the avian sinus petrosus caudalis, which also left a mark in the parietal. This part of the groove is exposed dorsally on the ventral aspect of the notch (Figs. 5F, 6A). At its lateral extremity, the groove bifurcates on the left side (Fig. 5D) but remains single on the right

side (Fig. 5C, E). The medial portion of the groove may have accommodated the trigeminal-anterior semicircular vein system (Seldmayr, 2002), which corresponds with various veins in birds (vena nervi trigemini, sinus petrosus anterioris, vena semicircularis anterioris; Baumel, 1993) and the vena cerebri media in non-avian reptiles (O'Donoghue, 1920; Romer, 1956). The sulcus of the trigeminal-anterior semicircular vein system continues on the intracranial surface of the supraoccipital in *Panphagia*, where it extends across the eminentia canalis semicircularis from the notch of the vena occipitalis externa towards the prootic (Figs. 5B, 6C). In posterodorsal and dorsal views, this portion of the groove is almost completely hidden by the parts of the supraoccipital immediately dorsal to the notch (Figs. 5F, 6A), as in *Massospondylus* (Gow, 1990:fig. 6A). Two conspicuous foramina open near the 'turn' of the groove within the pocket, the first located near the union with the lateral channel and the second located near the union with the intracranial channel (Fig. 5E).

The fossa cerebelli is located on the intracranial surface of the supraoccipital and housed the sinus occipitalis and cerebellum

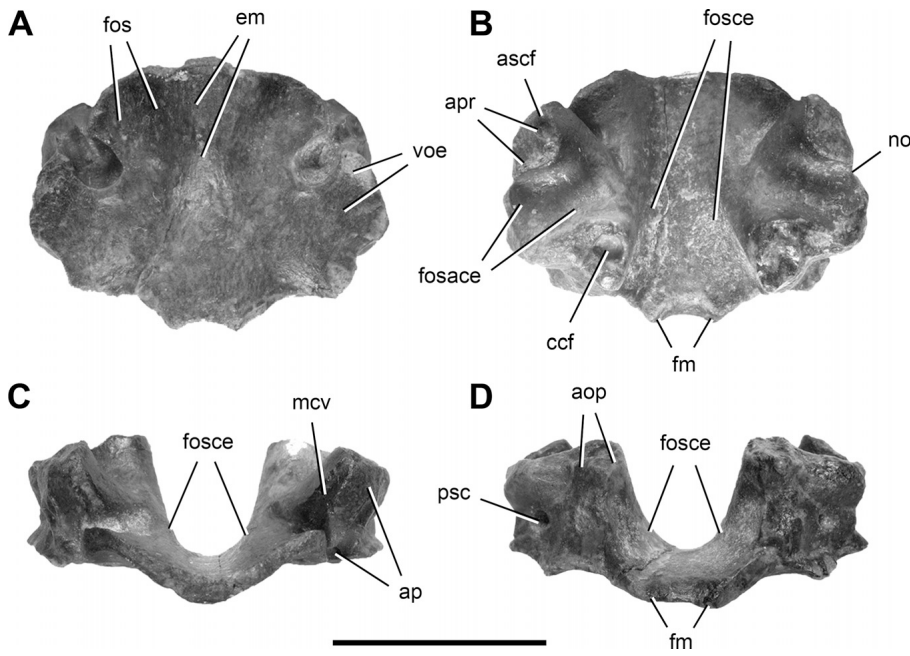


FIGURE 6. Supraoccipital of *Panphagia protos* (PVSJ 874) in posterodorsal (A), anteroventral (B), anterodorsal (C), and posteroventral (D) views. Anterior is towards the top of the page in A and B. **Abbreviations:** aop, articular surface for the exoccipital-opisthotic; ap, articular surface for the parietal; apr, articular surface for the prootic; ascf, anterior semicircular channel foramen; ccf, crus commune foramen; em, eminence; fm, foramen magnum; fos, fossa; fosace, fossa auriculariae cerebelli; fosce, fossa cerebelli; mcv, medial cerebral vein; no, notch; psc, posterior semicircular canal; voe, vena occipitalis externa. Scale bar equals 1 cm.

(Figs. 5B, G, 6B). A small, dorsoventrally elongate fossa extends ventromedially from the notch to the dorsal edge of the fossa auriculariae cerebelli (Figs. 5B, 6B). The supraoccipital portion of the fossa auriculariae cerebelli is deep, surrounded by the eminentia canalis semicircularis, an anterolaterally oriented convexity (Figs. 5B, 6B). The posterodorsal portion of the canalis semicircularis anterioris and the crus osseum commune are enclosed in this swelling (Evans and Martin, 1993).

The sutural articulation for the exoccipital-opisthotic is composed by two rugose surfaces, one facing ventrolaterally (Figs. 5A, C, D, G, 6D) and the other laterally (Fig. 5C, D). The ventrolateral surface is approximately square in shape and presents on its lateral region the foramen for the canalis semicircularis caudalis (Fig. 6D). The lateral surface is subrectangular with a dorsoventrally extended fossa (Fig. 5D, E). This surface and its fossa are

anterodorsally limited by a sulcus housing the sinus petrosus caudalis (Fig. 5C, D). The sulcus, which is located on a prominence on the lateral surface of the supraoccipital, lies adjacent to an articular surface for the parietal.

Another 'C'-shaped articular surface faces anteroventrally and exposes in cross-section the eminentia canalis semicircularis (Fig. 6B). The ventral extremity bears the foramen for the crus osseum commune (Fig. 6B) and a notch (Figs. 5C, D, 6B), which probably formed the dorsal part of the auricular foramen (Seldmayr, 2002). The lack of fit between the 'C'-shaped articular surface and the prootic suggests that there might have been intervening cartilage. Alternatively, the articulation may have accommodated both the prootic (posteriorly) and exoccipital-opisthotic, as in other non-avian dinosaurs (e.g., *Hypsilophodon*; Galton, 1974:fig. 9B, C). The foramen for the crus osseum

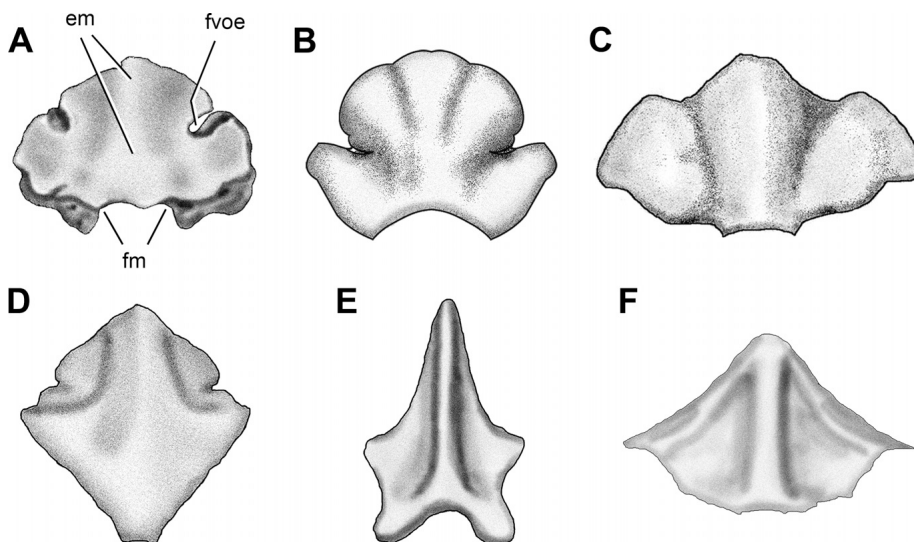


FIGURE 7. Posterior view of the supraoccipital of the basal dinosaurs *Panphagia* (A), *Adeopapposaurus* (B), *Thecodontosaurus* (YPM 2192) (C), *Melanorosaurus* (D), *Heterodontosaurus* (E), and *Herrerasaurus* (F). Modified from Martínez, 2009 (B); Benton et al., 2000 (C); Yates, 2007 (D); Norman et al., 2011 (E); and Sereno and Novas, 1994 (F). **Abbreviations:** em, eminence; fm, foramen magnum; fvoe, foramen for the vena occipitalis externa. The drawings are not in the same scale.



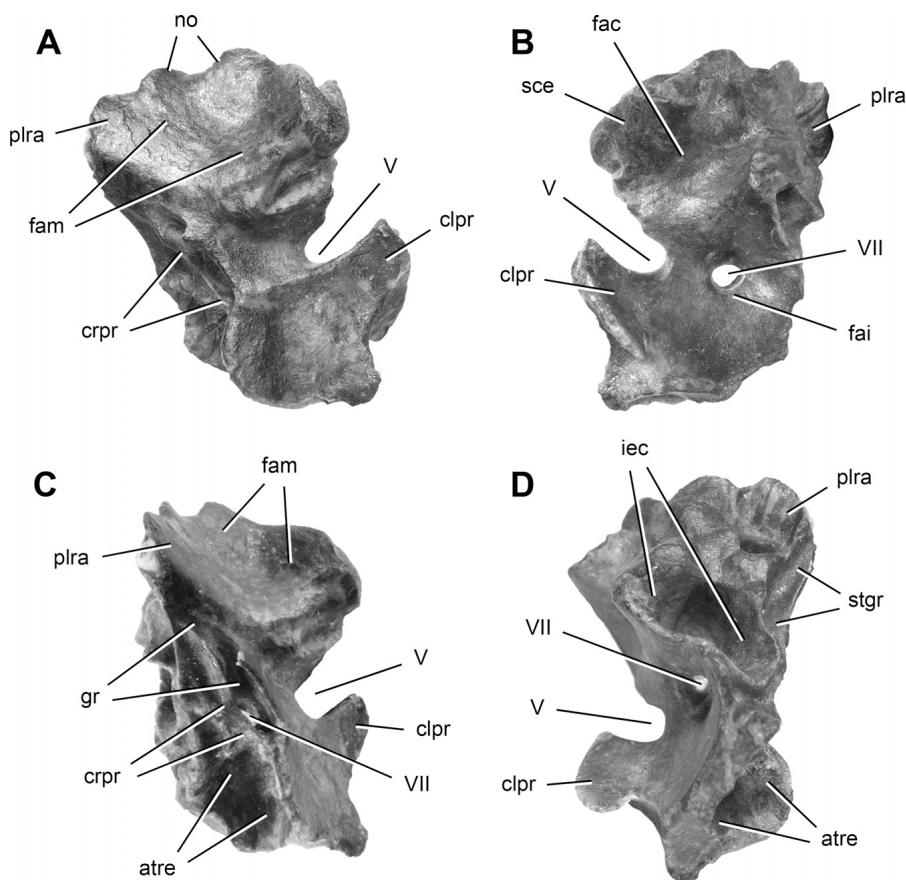


FIGURE 8. Right prootic of *Panphagia protos* (PVSJ 874) in lateral (A), medial (B), postero-lateral (C), and posterior (D) views. **Abbreviations:** atre, anterior tympanic recess; clpr, clinoid process; crpr, crista prootica; fac, fossa auricularae cerebelli; fai, fossa acustica interna; fam, fossa for the adductor mandibulae; gr, groove; iec, inner ear cavity; no, notch; plra, posterolateral ramus; sce, semicircular canal eminence; stgr, stapedial groove; V, VII, openings for cranial nerves V and VII. Scale bar equals 1 cm.

commune is slightly larger than the foramina for the canales semicirculares ossei anterioris and caudalis.

Comparing the proportionately broad supraoccipital of *Panphagia* with that in other basal dinosaurs, it is similar to that in most basal sauropodomorphs, such as *Efraasia*, *Anchisaurus*, *Adeopapposaurus* (Fig. 7B), and *Thecodontosaurus* (Fig. 7C). The supraoccipital has subequal proportions in *Silesaurus* (Dzik, 2003) and most basal dinosaurs such as *Herrerasaurus* (Fig. 7F), *Lesothosaurus* (Thulborn, 1970; Knoll, 2002a), and *Melanorosaurus* (Fig. 7D). The supraoccipital appears to be deeper than broad in *Heterodontosaurus* (Fig. 7E). A shallow median nuchal eminence (Figs. 5A, 6A, 7A) is similar to that in other basal sauropodomorphs, such as the *Thecodontosaurus* (Fig. 7C), *Eoraptor* (PVSJ 512), and *Adeopapposaurus* (Fig. 7B). The nuchal eminence is more prominent in *Melanorosaurus* (Fig. 7D) and other sauropodomorphs (*Platiosaurus*, Galton, 1984:fig. 4D; *Massospondylus*, Hinić, 2002). In the basal theropods *Herrerasaurus* (Fig. 7F), *Megapnosaurus kayentakatae* (Tykoski, 1998:fig. 9A, B), and *Majungasaurus* (Sampson and Witmer, 2007:fig. 14G), in contrast, the eminence is very prominent. The narrow contribution of the supraoccipital to the foramen magnum is also present in *Herrerasaurus* (Sereno and Novas, 1994:figs. 1G, 7C, 8C; Fig. 7F) and *Melanorosaurus* (Yates, 2007:fig. 8), in contrast to the slightly broader condition in *Lesothosaurus* (Sereno, 1991:figs. 11C, 12C) and the much broader condition present in *Adeopapposaurus* (Fig. 7B) and *Heterodontosaurus* (Norman et al., 2011:fig. 14). The foramen for the crus osseum commune is slightly larger than the foramina for the canales semicirculares ossei anterioris and cau-

dal is present in a juvenile *Massospondylus* specimen (Gow, 1990:fig. 6A). This condition contrasts with the wide vestibulum present in the supraoccipital of *Pantyraco* (Galton and Kermack, 2010:fig. 8A), *Hypsilophodon* (Galton, 1974:fig. 9B, C), and the basal archosauromorph *Prolacerta* (Evans, 1986). The large fossa cerebelli (= floccular recess) of *Panphagia*, which continues in the prootic (Figs. 5B, G, 6B), is absent in most sauropods.

**Prootic**—We describe the prootic, which is preserved on the right side, with its long axis positioned at 45° to the horizontal (Figs. 8, 9). The prootic has two fossae dorsal and ventral to a notch and groove for cranial nerve V visible in lateral view (Fig. 5A). The lateral surface of the dorsal region is concave and ventrally delimited by a thick and curved ridge. In other dinosaurs, this fossa has been interpreted either as the recessus tympanicus dorsalis (Baumel and Witmer, 1993; Witmer, 1997) or a surface for attachment of the *M. adductor mandibularis externus profundus* (Vanden Berge and Zweers, 1993; Holliday, 2009).

The undulating dorsal margin of the prootic, which contacted the parietal, has two convexities separated by three concavities. The posterior concavity (Fig. 8A) may represent the ventral border of the opening for the vena parietalis, as suggested in *Platiosaurus* (Huene, 1926:pl. 1, fig. 10; Galton and Kermack, 2010), or a pneumatic opening, as suggested in *Megapnosaurus kayentakatae* (Tykoski, 1998:fig. 10B). A pair of grooves converge posteroventrally just above the notch for cranial nerve V (Fig. 8A). The anteroventral one likely represents the path of the vena nervi trigemini, as in *Pantyraco* (Galton and Kermack, 2010). In *Massospondylus* (Gow, 1990:fig. 6A, B) and *Adeopapposaurus* (PVSJ 568), the groove leads to a notch on the anterior border.

An articular surface for the laterosphenoid between the vein sulcus and the notch for cranial nerve V is not present in *Panphagia*, similar to the condition in *Massospondylus* (Gow, 1990:figs. 3A, 6A). The notch for cranial nerve V is deep and anterodorsally directed (Fig. 8A, B). The anteroventral and posterodorsal borders of the notch are nearly parallel in lateral and medial views.

The clinoid process (Fig. 8A, B) has a distinctive subtriangular shape in lateral view. A ridge on the clinoid process along the anteroventral border of the notch for cranial nerve V continues posterovertrally to a subrectangular prominence and adjacent trough (Fig. 8A). This depressed area probably represents the path of the most proximal section of the mandibularis branch of cranial nerve V. The posterior border of this surface forms the anterior border of the external foramen for cranial nerve VII (Fig. 8A). Ventral to the trigeminal notch and groove is a smooth, trapezoidal surface for origin of the *M. protractor pterygoidei et quadrati* (Vanden Berge and Zweers, 1993) (Fig. 8A).

The external opening of cranial nerve VII is located on the crista prootica, slightly ventral to the opening for cranial nerve V (Fig. 8A). The oval foramen is bounded by sharp ridges with protuberances partially separating the foramen into posterodorsal and anteroventral portions (Fig. 8A, C). The smaller, posterodorsal portion would have lodged the nervus hyomandibularis (Dubbeldam, 1993), a branch of cranial nerve VII, the anteroventral portion of which may represent the exit of the nervus palatinus (Fig. 8A). The limiting ridges continue posterodorsally beyond the foramen, bounding a narrow sulcus that would have housed the most proximal portion of the nervus hyomandibularis.

A large anterior tympanic recess is located posteromedially to, and overlapped by, an attachment surface for the *M. protractor pterygoidei et quadrati* and ventrally to the foramen for cranial nerve VII. This fossa is broad, deep, and approximately circular in posterior view (Fig. 8D). Posterior to the foramen for cranial nerve VII and the crista prootica, the lateral surface of the prootic is reduced to a narrow area (Fig. 8A). This surface corresponds to a wall laterally overlapping the anterior border of the fenestra vestibuli (Baumel and Witmer, 1993; fenestra ovalis, sensu Romer, 1956). From the dorsal region of this area, a short sulcus extends posteriorly just medial and approximately parallel to the narrower sulcus for the nervus hyomandibularis (Fig. 8C).

In medial view, the dorsal part of the prootic bears the anteroventral portion of the fossa auriculae cerebelli (Fig. 8B). This fossa is anterodorsally limited by the eminentia canalis semicircularis (Fig. 8B) and ventrally limited by the medial wall of the auditory bulla (Oelrich, 1956). The auditory bulla is a bony capsule surrounding the vestibular recess and is notably inflated towards the cavum cranii (Fig. 8B), as in *Pantyrdraco* (Galton and Kermack, 2010:fig. 8F). Immediately anteroventral to the auditory bulla, there is a wide fossa acustica interna (Baumel and Witmer, 1993) into which open two foramina, one immediately dorsal to the other (Fig. 8B). The smaller, dorsal foramen is located on the ventral border of the auditory bulla and provided passage to the anterior ramus (Dubbeldam, 1993) of the nervus vestibulocochlearis (cranial nerve VIII), which opens into the anterior ampullar recess (Oelrich, 1956). The larger, ventral foramen provided passage to the undivided root of the nervus facialis (cranial nerve VII). Anterior to the notch for the nervus trigeminus (cranial nerve V) on the medial aspect of the clinoid process, the prootic presents a medially directed, fan-shaped lamina, which forms the dorsolateral part of the dorsum sellae (Baumel and Witmer, 1993) (Fig. 8B, D). The dorsomedial edge of this transverse lamina is sharp and convex (Fig. 8D) and likely did not contact its paired opposite except at its ventral extremity. The ventral border has a ventromedially directed notch (Fig. 8D) that forms the dorsolateral portion of the nervus abducens (cranial nerve VI). Anterior

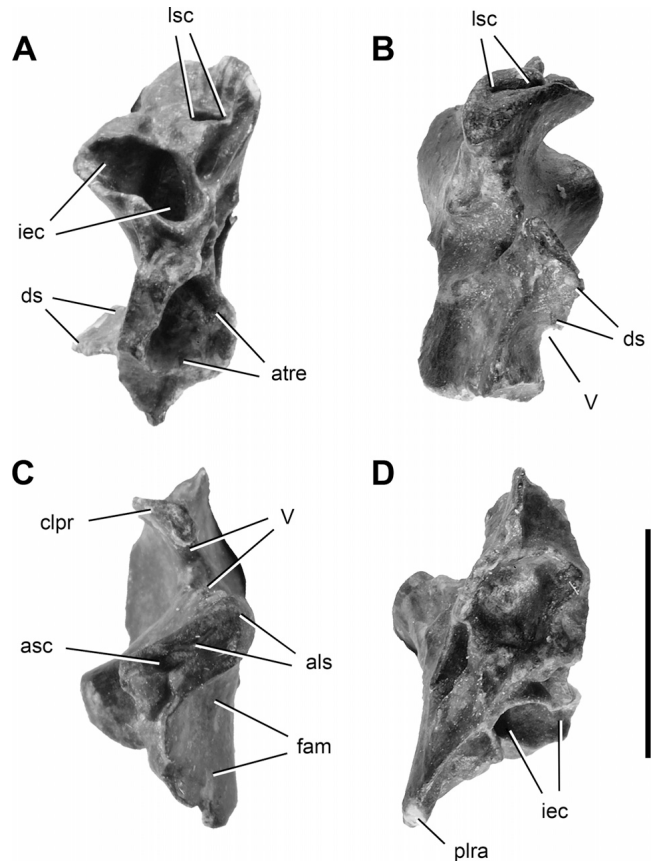


FIGURE 9. Right prootic of *Panphagia protos* (PVSJ 874) in posterovertral (A), anterior (B), dorsal (C), and ventral (D) views. **Abbreviations:** als, articular surface for the laterosphenoid; asc, anterior semicircular canal; atre, anterior tympanic recess; clpr, clinoid process; ds, dorsum sellae; fam, fossa for the adductor mandibulae; iec, inner ear cavity; lsc, lateral semi-circular canal; plra, posteriorolateral ramus; V, opening for cranial nerve V. Scale bar equals 1 cm.

to this lamina, the medial surface of the prootic faces the fossa hypophyseos (Fig. 8B).

In dorsal view, the anterodorsal surface of the prootic is approximately rectangular (Fig. 9C). This anterolaterally elongate surface has a foramen for the canalis semicircularis anterioris and several narrow sulci (Fig. 9C). It articulates with the posteromedial portion of the supraoccipital and anterolateral portion of the laterosphenoid.

The posteromedial surface of the prootic has a broad, rugose articular surface for the exoccipital-opisthotic dorsolateral to the vestibule (Fig. 8B, D). It houses the foramen for the canalis semicircularis lateralis (Evans and Martin, 1993) (Fig. 8D). The walls of the anterior portion of the canalis semicircularis lateralis, therefore, are completely surrounded by the prootic. In *Pantyrdraco*, in contrast, the prootic does not form the medial wall of this canal (fide Galton and Kermack, 2010). In *Panphagia*, this foramen is much larger than the preserved foramina for the canalis semicircularis anterioris and crus osseum commune. Posterolateral to this foramen, striae are present that parallel the long axis of the process (Fig. 8B, D).

The anteroventral surface of the prootic (Fig. 9D) has an articular surface for the anterior portion of the parabasisphenoid (sensu Gower, 2002). The smooth, concave articular surface is

subtriangular and has a straight lateral border. It forms the ventral edge of the attachment area for the *M. protractor pterygoidei et quadrati*. The strongly concave posteroventral border forms the ventral edge of the recessus tympanicus anterioris. The medial border forms the ventral edge of the endocranial surface of the prootic, which is slightly convex in ventral view (Fig. 9D). The posteromedial corner of the surface is anteroposteriorly elongated, medial to the anterior tympanic recess. The posterior surface of the prootic bears a rugose sutural area, most likely for the parabasisphenoid (Fig. 8D). In lateral view, the subquadrate sutural surface is concave and is marked by a small, conical fossa (Fig. 8D).

A spacious inner ear cavity opens between the posteriorly facing articular surfaces for the exoccipital-opisthotic and parabasisphenoid (Fig. 8D). The cavity is subconical, narrowing anteriorly (Fig. 8D). Within the cavity, a slight constriction differentiates the vestibulum posteriorly from the smaller ampulla ossea lateralis anteriorly (sensu Evans and Martin, 1993). In posterior view, the vestibular recess is subelliptical, with its long axis oriented dorsomedially (Fig. 8D). On the ventromedial surface of the ampulla ossea lateralis, a foramen is present for the anterior ramus of the nervus vestibulocochlearis (cranial nerve VIII) or perhaps only the nervus ampullaris lateralis (Dubbeldam, 1993). The foramen for the canalis semicircularis lateralis opens dorsolaterally on the ampulla ossea lateralis. Anterior view of the ampulla ossea anterioris is obscured by matrix. A small notch for the ramus caudalis (sensu Dubbeldam, 1993) of the nervus vestibulocochlearis (cranial nerve VIII) is present on the posterior border of the vestibular recess (Fig. 8B), as in *Plateosaurus* (Galton, 1985:fig. 7G). A notch on the posterior border of the lateral wall of the vestibular recess forms the anterior margin of the fenestra vestibuli (Fig. 8B, C). A posteroventrally directed depression, the recessus columellae (sensu Baumel and Witmer, 1993) (Figs. 8C, D, 9D), is present dorsolateral to the fenestra vestibule and continues posterolaterally to join the stapedial groove (sensu Sampson and Witmer, 2007) on the ventral aspect of the posterolateral process (Figs. 8D, 9D). The stapedial groove likely continued distally onto the paroccipital process of the opisthotic.

Comparing the prootic of *Panphagia* with that in other basal dinosaurs, the surface for the origin of the *M. protractor pterygoidei et quadrati*, which corresponds to the lateral surface of the prootic ventral to the notch for the cranial nerve V, is anteroposteriorly wider than dorsoventrally high. The ratio between the length of this area along the long axis of the prootic to the length along its orthogonal axis in the sagittal plane is greater than in *Silesaurus*, *Lesothosaurus*, and more derived sauropodomorphs, but less than in the basal theropod *Tawa* (Table 1). The opposing borders of the notch for cranial nerve V are nearly parallel in lateral and medial views (Fig. 8A, B) in *Panphagia*, which is similar to that in *Massospondylus* (Gow, 1990:fig. 6A) and *Plateosaurus* (Galton, 1984:fig. 4B). In other non-avian di-

nosaurus and immediate outgroups, the borders of the notch either converge anterodorsally (*Silesaurus*, Dzik, 2003:fig. 7A, B; *Coelophysus*, Raath, 1985:fig. 1A; *Melanorosaurus*, Yates, 2007:fig. 11A, B) or diverge (*Pantydraco*, Galton and Kermack, 2010:fig. 8D, E, G; Yates, 2003:fig. 7A, B). The external opening of cranial nerve VII on the crista prootica is situated somewhat ventral to the level of cranial nerve V (Fig. 8A), a topology found in many basal sauropodomorphs (e.g., *Adeopapposaurus*, Martínez, 2009:fig. 10C; *Pantydraco*, Galton and Kermack, 2010:fig. 8E; *Massospondylus*, Gow, 1990:fig. 6A, B) and basal theropods (e.g., *Coelophysus*, Raath, 1985:fig. 1A). The anterior tympanic recess of *Panphagia* (Fig. 8D) is similar to that in neotheropods (Witmer, 1997) and larger than that in some other basal sauropodomorphs (e.g., *Adeopapposaurus*; PVSJ 568). Sauropods appear to lack the anterior tympanic recess altogether.

## DISCUSSION

### Specimen Maturity

The subadult status of the holotype of *Panphagia* is inferred from the lack of fusion of the preserved braincase elements, open neurocentral sutures in presacral vertebrae, and the open scapulocoracoid suture (Brochu, 1995; Irmis, 2007; Martínez and Alcobér, 2009). Some features of the preserved braincase elements, in addition, are consistent with subadult status, such as the absence of a precise articular match between the supraoccipital and prootic. The edges of these bones may have yet to fully ossify near their sutural junction (DeBeer, 1937). The proportionately large size of the notches in the supraoccipital for the vena occipitalis externa resembles the condition in subadult *Massospondylus* (Gow, 1990; for adult form, see Sues et al., 2004). The medial edge of the parietals in *Panphagia* suggests that there was a median foramen, which has been cited as an indication of immaturity in ornithischians (Knoll, 2002b). Pol and Powell (2007) and others have noted, however, that many adult sauropodomorphs retain this foramen.

### Soft-Tissue Considerations

The fossa on the lateral surface of the prootic has been alternatively interpreted either as a muscular attachment site (Raath, 1985; Holliday, 2009:fig. 5A–C) or a pneumatic feature related to the recessus tympanicus dorsalis (Witmer, 1997). Rauhut (2004) considered both interpretations equally plausible. The shape and position of the fossa resembles the attachment site for the *M. adductor mandibularis externus profundus* in *Ctenosaura* (Oelrich, 1956). This interpretation may be more reasonable, given the general absence of prominent pneumatic features (Smith et al., 2007). On the other hand, the *M. adductor mandibularis externus profundus* does not attach to the prootic in extant archosaurs (Holliday and Witmer, 2007), which also have extensive pneumatic features in this region. In the light of this bracket of extant outgroups (Witmer, 1995b), we regard the pneumatic hypothesis as the more likely.

### Comparisons

The braincase is the source of little character evidence at basal nodes within Dinosauria (e.g., frontal contribution to the supratemporal fenestra [Gauthier, 1986]; depth of the occipital wing of the parietal [Wilson and Sereno, 1998]; position of foramina for mid-cerebral vein on occiput [Yates, 2003]). The paucity of characters reflects the limited information available on the braincase in many basal dinosaurs. When preserved, the braincase is only rarely exposed, and isolated braincase elements that offer a

TABLE 1. Ratio of the length of surface for the origin of the *M. protractor pterygoidei et quadrati* along the long axis of the prootic and along its orthogonal axis in the sagittal plane in several dinosauriforms.

Taxon	Source	Ratio
<i>Adeopapposaurus</i>	PVSJ 568	0.7
<i>Coloradisaurus</i>	Bonaparte, 1978	0.6
<i>Lesothosaurus</i>	Sereno, 1991	0.5
<i>Massospondylus</i>	Gow, 1990	0.7
<i>Panphagia</i>	PVSJ 874	0.9
<i>Pantydraco</i>	Benton et al., 2000	1.0
<i>Silesaurus</i>	Dzik, 2003	0.5
<i>Tawa</i>	Nesbitt et al., 2009	1.7

detailed assessment of foramina and fossae are particularly scarce. To the extent possible, we compare several features described above in the braincase of *Panphagia* with other basal dinosaurs.

**Sauropodomorph Affinity**—A few features of the braincase in *Panphagia* lend weak support for its inclusion within Sauropodomorpha. The broad proportions of the supraoccipital, which is broader transversely than deep dorsoventrally, is common among basal sauropodomorphs (Fig. 7A). The supraoccipital is deeper than broad or has subequal dimensions in other basal dinosaurs, such as *Herrerasaurus* (Sereno and Novas, 1994).

The nuchal crest is low in *Panphagia*, as in *Thecodontosaurus* (YPM 2192), *Adeopapposaurus*, and *Riojasaurus*. Given the larger body size of some of these taxa, this character may be size independent. A more prominent crest characterizes most theropods, ornithischians, and the basal dinosauriform *Silesaurus*.

The deeply incised notches in the supraoccipital for the vena occipitalis externa resemble the condition in many basal sauropodomorphs (e.g., *Plateosaurus*, *Massospondylus*, *Adeopapposaurus*, *Melanorosaurus*), but in contrast to the condition in theropods (e.g., *Herrerasaurus*, *Megapnosaurus kayentakatae*, *Coelophysis*) and ornithischians (e.g., *Lesothosaurus*, *Heterodontosaurus*). A deeply notched supraoccipital as in sauropodomorphs may be apomorphic, although deep notches are also present in the dinosaurian outgroup *Silesaurus* (Dzik, 2003).

The attachment area on the prootic for the M. protractor pterygoidei et quadrati has an elongate shape in *Panphagia*, similar to that in *Thecodontosaurus* (YPM 2192). The shape of this feature, however, has a complex distribution among dinosaurs. In *Silesaurus*, the basal ornithischian *Lesothosaurus*, and many sauropodomorphs (e.g., *Adeopapposaurus*, *Coloradisaurus*, *Riojasaurus*, *Massospondylus*), the attachment area is short, but in the basal theropod *Tawa* it is slightly longer than in *Panphagia*.

**Plesiomorphic Characters within Sauropodomorpha**—The frontal of *Panphagia* has a characteristic shape: it is elongate (length more than twice width at the level of the posterolateral process), with its anterior tip located closer to the midline than to the lateral border of the bone (Fig. 2A). Most basal dinosaurs (e.g., *Lesothosaurus*, *Herrerasaurus*, *Coelophysis*) including basal-most sauropodomorphs (e.g., *Eoraptor*, *Pantydraco*, *Pampadromaeus*) have a frontal of this form. In more derived sauropodomorphs, in contrast, the frontal is broader than long and the anterior tip is closer to the lateral border of the bone (e.g., *Plateosaurus*, *Massospondylus*, *Adeopapposaurus*, *Melanorosaurus*).

The large anterior tympanic and floccular recesses in *Panphagia* (Figs. 5B, G, 6B, 8D) are similar to those in neotheropods (Witmer, 1997). In at least some basal sauropodomorphs, such as *Adeopapposaurus*, these recesses are smaller, and they appear to be absent in sauropods. Both of these features suggest that *Eoraptor* and a few close relatives may constitute stem sauropodomorphs at or near the base of the clade.

## CONCLUSIONS

The disarticulated braincase elements of a subadult specimen of *Panphagia protos* provide new information on the morphology of the braincase in an early sauropodomorph dinosaur. A few features of the braincase link *Panphagia* with other sauropodomorphs, and a few other features suggest that *Panphagia* may be more primitive than basal sauropodomorphs such as *Plateosaurus* or *Massospondylus*. The former includes a proportionately elongate frontal, and the latter includes the presence of anterior tympanic and floccular recesses. The significance of these features will be easier to assess when additional information on the braincase is available for other basal dinosaurs.

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