A Basal Sauropodomorph (Dinosauria: Saurischia) from the Ischigualasto Formation (Triassic, Carnian) and the Early Evolution of Sauropodomorpha

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Abstract

Background: The earliest dinosaurs are from the early Late Triassic (Carnian) of South America. By the Carnian the main clades Saurischia and Ornithischia were already established, and the presence of the most primitive known sauropodomorph Saturnalia suggests also that Saurischia had already diverged into Theropoda and Sauropodomorpha. Knowledge of Carnian sauropodomorphs has been restricted to this single species.

Methodology/Principal Findings: We describe a new small sauropodomorph dinosaur from the Ischigualasto Formation (Carnian) in northwest Argentina, Panphagia protos gen. et sp. nov., on the basis of a partial skeleton. The genus and species are characterized by an anteroposteriorly elongated fossa on the base of the anteroventral process of the nasal; wide lateral flange on the quadrate with a large foramen; deep groove on the lateral surface of the lower jaw surrounded by prominent dorsal and ventral ridges; bifurcated posteroventral process of the dentary; long retroarticular process transversely wider than the articular area for the quadrate; oval scars on the lateral surface of the posterior border of the centra of cervical vertebrae; distinct prominences on the neural arc of the anterior cervical vertebra; distal end of the scapular blade nearly three times wider than the neck; scapular blade with an expanded posterodistal corner; and medial lamina of brevis fossa twice as wide as the iliac spine.

Conclusions/Significance: We regard Panphagia as the most basal sauropodomorph, which shares the following apomorphies with Saturnalia and more derived sauropodomorphs: basally constricted crowns; lanceolate crowns; teeth of the anterior quarter of the dentary higher than the others; and short posterolateral flange of distal tibia. The presence of Panphagia at the base of the early Carnian Ischigualasto Formation suggests an earlier origin of Sauropodomorpha during the Middle Triassic.

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Introduction

Basal Dinosauria

The early evolution of the Dinosauria, including the split between its two main clades Saurischia and Ornithischia, remains poorly understood because of the scarcity of fossiliferous terrestrial beds covering the late Middle Triassic (Ladinian) and early Late Triassic (Carnian). The best preserved record of Ladinian continental tetrapod assemblages comes from the Chañares Formation in Northwestern Argentina. The representative fauna includes the best known sister taxa of Dinosauria, the dinosaurs *Marasuchus lilloensis* [3,4] and *Saturnalia* [5], which present apomorphies that suggest also that Saurischia had already diverged into Theropoda and Sauropodomorpha.

Carnian basal saurischians dinosaurs

Carnian basal saurischian dinosaurs are scarce and frequently fragmentary. Most are from South America, except the fragmentary *Aliwathera malenesis* [10] from India. The most complete and better known skeletons were found in the Carnian Ischigualasto Formation in Northwestern Argentina. This record includes *Herrerasaurus ischigualastensis* (=Fengellosaurus ischigualastensis and *Ichisaurus cattai*), *Eoraptor lunensis* [8,11–13], and three new undescribed taxa [14–16]. To the Carnian Upper Santa María Formation in Brazil belong the fragmentary herrerasaurid *Staurikosaurus pricei* [17] and the basal sauropodomorph *Saturnalia tepuyensis* [18]. Although *Saturnalia* presents apomorphies that confirm that it is a sauropodomorph (relatively short head, long and narrow ventral rami of the squamosal, high tooth crowns on
the anterior quarter of the tooth-bearing areas and broad distal humerus) [19], it retains morphological characters that indicate a basal position within Sauropodomorpha. Those characters are the straight dentary, fine and straight tooth serrations, tibia longer than the femur, presence of trochanteric shelf, and fourth trochanter placed proximally on the shaft of the femur, among others. Knowledge of pre-Norian sauropodomorph evolution has been restricted to this single species.

We report here a new primitive sauropodomorph dinosaur from the lower levels of the Ischigualasto Formation (Carnian) in San Juan Province, Argentina. The remains consist of one incomplete, partially disarticulated skeleton unearthed during the 2006 field season of the Museo de Ciencias Naturales of San Juan in Ischigualasto Provincial Park.

Methods
Preparation
The holotype was prepared using pneumatic air scribe, pin vice and water immersion. The red-brown-colored bones were encased in a grey-green fine-grained sandstone matrix with calcareous cement. Several pieces were encased in light-grey calcareous concretions.

Terminology
We employ traditional, or “Romerian,” anatomical and directional terms over veterinarian alternatives [20]. “Anterior” and “posterior,” for example, are used as directional terms rather than the veterinarian alternatives “rostral” or “cranial” and “caudal”. We also follow recent recommendations regarding the identification of vertebral laminae [21].

We used the phylogenetic definitions for basal taxa within Dinosauria proposed by Sereno [22]. Sauropodomorpha, for example, has a stem-based definition in opposition to Theropoda and does not require the monophyly of Saurischia or Prosauropoda (as defined, for example, by Galton and Upchurch [23]). In this way, Sauropodomorpha is defined as “The most inclusive clade containing Saltasaurus loricatus but not Passer domesticus, nor Triceratops horridus.”

Institutional abbreviations.
BRMSG Bristol City Museum and Art Galleries, Bristol, United Kingdom.
PVSJ Instituto y Museo de Ciencias Naturales, San Juan 5400, Argentina.
YPM Peabody Museum of Natural History, Yale University, New Haven, United States of America.

Results
Systematic Paleontology
Systematic hierarchy.
Dinosauria Owen, 1842
Saurischia Seeley, 1887
Sauropodomorpha Huene, 1932
Panphagia genus nov.

Etymology. Pan (all, Greek); phagein, to eat (Greek); ia, pertaining to (Greek). In reference to the inferred omnivorous diet of the new taxon, which appears to be transitional between carnivory and herbivory.

Type species. Panphagia protos.

Panphagia protos species nov.

Etymology. Protos, first (Greek). In reference to the basal position of the new taxon within Sauropodomorpha.

Holotype. PVSJ 874; partial skull including the right nasal and prefrontal, left frontal, both parietales, both quadrates, right prootic, supraoccipital, anterior half of the left lower jaw, and right lower jaw lacking the anterior tip of the dentary; axial remains includes one anterior and two posterior cervical vertebrae, four posterior dorsal neural arches, one dorsal centrum, first prordial sacral vertebrae, two proximal, one proximo-medial, and 15 distal caudal vertebrae; appendicular elements include the left scapula, left ilium, left pubic apron, left ischium, right tibia and astragulas, right metatarsal 3, proximal half of probable left metatarsal 4, and four pedal phalanges of uncertain position, one of which is an ungaull. The bones were found disarticulated but in close association over an area of 1 m². The specimen is an immature individual that has open neurocranial, neurocentral and scapulocoracoid sutures and an estimated body length of approximately 1.30 m.

Type Locality. Valle Pintado, Hollanda de Ischigualasto, Ischigualasto Provincial Park, San Juan Province, Argentina (Figure 1).

Horizon and Age. 40 m above the base of the Ischigualasto Formation, Carnian (ca. 228.3 Mya) [7], Ischigualasto–Villa Unión Basin. The holotypic layer is approximately at the same level of the dated ash, which implies a Lower Carnian age for the specimen.

Diagnosis. Dinosaur characterized by an anteroposteriorly elongated fossa on the base of the anteroventral process of the nasal; wide lateral flange on the quadrates with a large foramen located far from the shaft; deep groove on the lateral surface of the lower jaw surrounded by prominent dorsal and ventral ridges, extending from the position of ninth tooth to the surangular foramen; posteroventral process of the dentary bifurcated in two slender rami that overlap the lateral surface of the angular; long retroarticular process of the articular transversally wider than the articular area for the quadrate; oval scars on the lateral surface of the posterior border of the centra of cervical vertebrae; distinct prominences located posteroventrally on the diapophyses of the neural arc of the anterior cervical vertebrae; distal end of the scapula blade nearly three times wider than the neck; scapula blade with an expanded postero dorsal corner limited by a wedged posterior border; and medial lamina of brevis fossa twice wider than the iliac spine.

These features distinguish Panphagia protos from known basal sauropodomorphs such as Satamalia tupiniquim and other basal saurischians as Eoraptor lunensis.

Description
Although the specimen was found in disarticulation with the exception of the 15 distal caudal vertebrae, the proximity of all pieces, the agreement in size between the different bones, and the absence of any duplicate elements all suggest these bones pertain to a single individual (Figure 2). All the limb bones and vertebrae have hollow shafts as in Eoraptor, Herrerasaurus, the basal sauropodomorph BRMSG Ca7456 [24], and neotheropods. The skeletal size and general proportions resemble those of Eoraptor. Nevertheless, Panphagia is slightly larger, axially more elongated, and has relatively shorter hindlimb bones than Eoraptor (Tables 1, 2).

Crani. The nasal is proportionally short, measuring less than half the length of the cranium as in Eoraptor and basal sauropodomorphs [23] but shorter than that in Herrerasaurus [12] and the neotheropods “Syntarsus” [25] and Coelophysis [26]. The lateral border of the nasal is slightly concave (Figure 3B) and differs from the convex border of Eoraptor. The interparial process arches above the margin of the skull in lateral view (Figure 3A) as in
Eoraptor and some basal sauropodomorphs such as Plateosaurus [27] and Lufengosaurus [28]. An anteroposteriorly elongated fossa is located on the base of the subtriangular anteroventral process (Figure 3A), which is not present in Eoraptor or Herrerasaurus. There is a well-developed posterolateral process of the nasal (Figure 3B) as in Eoraptor, basal theropods and sauropodomorphs [19].

The prefrontal (Figure 3C) is L-shaped, with a concave orbital surface and slightly convex dorsal surface as in Eoraptor. The posterior process fits on a deep groove on the anterolateral surface of the frontal (Figure 3D).

The frontal is narrow between the orbits as in Eoraptor (Figure 3D), unlike the wide frontal of Herrerasaurus. The posterior part of the dorsal surface forms the anterior wall of the supratemporal fossa as in other dinosaurs [4]. The sutural surface for the anterodorsal process of the postorbital is a deep and narrow groove as in Eoraptor but differing from the wide sutural area of Herrerasaurus.

The parietal presents a slender posterolateral wing and a well-marked dorsal ridge that medially delimits the supratemporal fossa (Figure 3E). The dorsal ridges of both parietals converge...
Table 1. Dimensions (mm) of the axial bones of the holotypic specimen of Panphagia protos (PVSJ 874).

<table>
<thead>
<tr>
<th>Bone</th>
<th>Measurements</th>
<th>Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>skull</td>
<td>total length of nasal</td>
<td>58425 (r)</td>
</tr>
<tr>
<td></td>
<td>total length of frontal</td>
<td>43.2 (l)</td>
</tr>
<tr>
<td></td>
<td>maximal width of frontal</td>
<td>20.3 (l)</td>
</tr>
<tr>
<td></td>
<td>total length of parietal</td>
<td>23.55 (l)</td>
</tr>
<tr>
<td></td>
<td>height of quadrate</td>
<td>30.4 (l); 30.85 (r)</td>
</tr>
<tr>
<td></td>
<td>height of pterygoid wing</td>
<td>19 (l); 19.65 (r)</td>
</tr>
<tr>
<td></td>
<td>transverse width of supraoccipital</td>
<td>17.2</td>
</tr>
<tr>
<td></td>
<td>maximal length of supraoccipital</td>
<td>12</td>
</tr>
<tr>
<td>lower jaw</td>
<td>total length of lower jaw (estimated from both jaws)</td>
<td>121.05 (e)</td>
</tr>
<tr>
<td></td>
<td>total length of dentary (estimated from both jaws)</td>
<td>73.6e</td>
</tr>
<tr>
<td></td>
<td>height of dentary at mid-length</td>
<td>7.35 (l); 9 (r)</td>
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<tr>
<td></td>
<td>anteroposterior length of external mandibular fenestra</td>
<td>17.6 (r)</td>
</tr>
<tr>
<td></td>
<td>transverse width of quadrate facet on articular</td>
<td>9.15 (r)</td>
</tr>
<tr>
<td></td>
<td>maximal transverse width of retroarticular process behind articular facet</td>
<td>9.5 (r)</td>
</tr>
<tr>
<td></td>
<td>length of internal mandibular fenestra</td>
<td>28.35 (r)</td>
</tr>
<tr>
<td>Vertebral column</td>
<td>length of ventral contour of anterior cervical (4th?) centrum</td>
<td>25.65</td>
</tr>
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<td></td>
<td>total length of anterior cervical (4th?) vertebral</td>
<td>34.85</td>
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<td>total height of anterior cervical (4th?) vertebra</td>
<td>22.75</td>
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<td></td>
<td>length of ventral contour of posterior cervical (7th?) centrum</td>
<td>24.6</td>
</tr>
<tr>
<td></td>
<td>total height of posterior cervical (7th?) vertebra</td>
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<td>height of posterior dorsal neural arch</td>
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<td></td>
<td>maximal anteroposterior length of dorsal neural arch</td>
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<td>length of ventral contour of posterior dorsal centrum</td>
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<td>length of ventral contour of first primordial sacral centrum</td>
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<td></td>
<td>maximal height of first primordial sacral vertebra</td>
<td>45</td>
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<td>dorsoventral height of first primordial sacral rib iliac attachment</td>
<td>17.25 (l); 17.15 (r)</td>
</tr>
<tr>
<td></td>
<td>maximal anteroposterior length of first primordial sacral rib</td>
<td>23.9</td>
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Abbreviations: b, broken; e, estimated; l, left side; r, right side.
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The shaft of the quadrate is dorsoventrally bowed as in *Eoraptor* and unlike the straight quadrate of *Herrerasaurus*. The lateral flange is transversally wider than in *Eoraptor* and *Herrerasaurus*. The quadrate foramen is large and fully enclosed in a deep fossa located on the lateral flange, above the neck, at the same level of the ventral border of the pterygoid wing (Figure 3F). This foramen is located laterally on the wing and well separated from the shaft, which is different than its position proximal on the shaft found in *Herrerasaurus*, *Eoraptor*, basal sauropodomorphs and basal neotheropods. The pterygoid flange forms more than 70% of the quadrate height as in most basal sauirchians [29]. The quadrate condyle presents a well-developed sulcus of anteromedial direction, as in *Herrerasaurus* (PVSJ 53, holotype of *Fengelisaurus*) and *Plateosaurus* [30].

The supraoccipital is much wider than it is high (Figure 3G), as in *Herrerasaurus* and basal sauropodomorphs such as *Pantydraco* [29] and *Efraasia* [31]. As in *Eoraptor*, it presents a prominent nuchal crest on the posterior surface, above the dorsal border of the foramen magnum. The foramina for the vena capitis dorsalis form deep notches on the posterior surface near the laterodorsal border (Figure 3F), similar to the non-dinosaurian dinosauirform *Silesaurus* [6].

The prootic bears a wide trigeminal notch anteromedially located and presents a well defined anteroventral surface for the protractor pterygoideus muscle (Figure 3H). Medially it preserves parts of the internal ear.

**Lower jaw.** The lower jaw is proportionally more slender than in *Eoraptor*. The articulation of the lower jaw is located ventral to the tooth row, as in many sauropodomorphs and *Eoraptor* (Figure 4A, B). The length of the retroarticular process is greater than the depth of the mandible below the glenoid. The external mandibular fenestra is dorsoventrally pinched in its anterior portion as in *Eoraptor* and represents 16% of the mandibular length (Figure 4A). The reduction of the fenestra is also present in basal sauropodomorphs.

The dentary comprises more than 55% of the length of the lower jaw, as in *Eoraptor*, *Herrerasaurus* and many other basal sauirchians. The posterior half of the ventral border of the dentary is slightly concave in lateral view, similar to that of basal sauropodomorphs such as *Pantydraco*, *Plateosaurus* and *Massospondylus* and different from the straight ventral border of *Eoraptor* and the slightly convex border of *Herrerasaurus*. The anterior part of the dentary, from the anterior tip to the level of the fourth tooth, expands dorsoventrally as in the basal neotheropods *Coelophysis* and *Sinyavasaurus* [32] and to a lesser degree in *Herrerasaurus* and *Eoraptor*. Several large and deep neurovascular foramina open on the lateral surface of the dentary. They are located along a line parallel to the dorsal border, along the complete tooth series, but at the level of
the tenth dentary tooth, they are located inside of a deep groove that posteriorly reaches the anterior surangular foramen (Figure 4A,C). Two pronounced ridges border this groove dorsally and ventrally, being the latter the most prominent. A similar groove, but limited to the dentary and without the ridges is present in *Coelophysis rodhesiensis* [26]. The ventral ridge differs from that of other sauropodomorphs as *Thecodontosaurus* neotype [24], *Plateosaurus* [30], and *Coloradisaurus* [19], in being wider at mid-length of the tooth bearing area than at the posterior end of the dentary. The posteroventral process of the dentary is bifurcated into two slender branches that overlap the lateral surface of the angular; the dorsal one reaches the ventral border of the external mandibular fenestra, and the other reaches the ventral border of the lower jaw (Figure 4A).

The splenial covers the medial aspect of the dentary and the ventral part of the intercoronoid. The mylohyoid foramen is fully enclosed by the splenial and located anteroventrally. The posterior ramus medially overlaps the ventral border of the prearticular and the anterior process of the angular. The suture between the splenial, dentary and prearticular does not show evidence of the intramandibular joint.

The surangular forms most of the lateral surface of the posterior part of the lower jaw, and the dorsal and posterior borders of the external mandibular fenestra. A small foramen opens just anterior to the posterior surangular foramen, below the surangular ridge. As in other saurischians, a large anterior surangular foramen opens anteriorly on the dorsal border of the surangular, enclosed in an anteroposteriorly oriented groove. The anterodorsal process of the surangular extends well anterior to the external mandibular fenestra, as in *Eoraptor* and unlike the short process of *Herrerasaurus* and most basal sauropodomorphs such as *Plateosaurus* [30] and *Massospondylus* [33].

The articular forms the posterodorsal border of the lower jaw. Unlike any other saurischian, the long retroarticular process is transversally wider than the articular fossa for the quadrate condyles (Figure 4D). The articular fossa is oriented along an anteromedial-posterolateral axis. The angular extends anteriorly to its contact with the dentary and splenial at the level of the anterior border of the external mandibular fenestra. Posteriorly its distal tip is broken. Judging from the articular facet on the lateroventral border of the surangular, the slender posterior tip would have extended to the level of the retroarticular process. This long and slender posterior process of the angular is similar to that of *Eoraptor* and different from the short process of *Herrerasaurus*.

### Table 2. Dimensions (mm) of the girdle and limb bones of the holotypic specimen of *Panphagia protos* (PVSJ 874).

<table>
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<th>Length</th>
</tr>
</thead>
<tbody>
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<td>scapula</td>
<td>Total length</td>
<td>91.85(l)</td>
</tr>
<tr>
<td></td>
<td>anteroposterior width of distal blade</td>
<td>41.5 (l)</td>
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<tr>
<td></td>
<td>minimum anteroposterior width of blade neck</td>
<td>14.5 (l)</td>
</tr>
<tr>
<td></td>
<td>maximal length from acromion to glenoid</td>
<td>44.9 (l)</td>
</tr>
<tr>
<td>ilium</td>
<td>Length from pubic peduncle to postacetabular process</td>
<td>46.1 (l)</td>
</tr>
<tr>
<td></td>
<td>Maximum height from supraacetabular lip</td>
<td>15.8(l)</td>
</tr>
<tr>
<td></td>
<td>Transverse width of distal end of the postacetabular process</td>
<td>10.1(l)</td>
</tr>
<tr>
<td>pubis</td>
<td>length of pubic apron</td>
<td>78.65 (l)</td>
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<td></td>
<td>mid-length width of pubic apron</td>
<td>24.35 (l)</td>
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<td></td>
<td>proximal width of pubic apron</td>
<td>26 (l)</td>
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<td>dorsoventral thickness at mid-length</td>
<td>7.65 (l)</td>
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<td>dorsoventral thickness at distal end</td>
<td>17.6 (l)</td>
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<tr>
<td>tibia</td>
<td>total length</td>
<td>157 (r)</td>
</tr>
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<td></td>
<td>length of medial border of distal surface</td>
<td>18.15 (r)</td>
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<td>length of lateral border of distal surface</td>
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<td></td>
<td>length of posterior border of distal surface</td>
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<td>astragalus</td>
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<td>transverse width of fibular facet</td>
<td>3.7 (r)</td>
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<td>anteroposterior length of medial contour in dorsal view</td>
<td>19.15 (r)</td>
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<td>anteroposterior length of lateral contour in dorsal view</td>
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<td>anteroposterior length of lateral border of base of ascending process</td>
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<td>anteroposterior length of medial border of base of ascending process</td>
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<td>metatarsal 3</td>
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<td>7 (r)</td>
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<td></td>
<td>proximal articular surface anteroposterior width</td>
<td>15.7 (r)</td>
</tr>
<tr>
<td></td>
<td>transverse width of the distal end</td>
<td>12.85 (r)</td>
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Abbreviations: b, broken; e, estimated; l, left side; r, right side.
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Dentition. Only the dentary teeth are preserved. There are at least 23 alveoli on the left dentary (Figure 4C) and apparently 22 on the right (Figure 4A). The teeth of *Panphagia* are slightly constricted at the base (Figure 4C, 5A) as in basal sauropodomorphs and some of the teeth of *Eoraptor*. Another feature of the teeth is the presence of labial and lingual eminences that extend along the crown (Figure 5A, B). A similar eminence is present on the labial surface of the crowns of *Thecodontosaurus* neotype, and *Eoraptor*, although in the latter the lingual surfaces are unexposed. As in other basal sauropodomorphs, the teeth of *Panphagia* have coarse oblique serrations on the anterior and posterior margins (Figure 5C) that differ from the fine, perpendicular serrations present in *Saturnalia* [19] and basal saurischians. The morphology and arrangement pattern are different between the anterior quarter and the rest of the tooth series, with a fairly abrupt transition occurring after the fourth or fifth tooth (Figure 4C). This is best observed in the left rather than the right jaw, as the latter has crowns that are dislodged from their alveoli. The anterior teeth are longer than the posterior, as in *Saturnalia* [34] and most basal sauropodomorphs. They are also less basally constricted, and more posteriorly recurved. The posterior teeth are smaller, more leaf-shaped, and present more marked serrations. Although the size of each tooth is similar, the height of the crown gradually decreases backwards. They are also closely apressed in a subimbricated pattern, whereas the anterior ones are more spaced. Again, this can be best seen in the left jaw, where the teeth are in their original position.

Axial skeleton. Three disarticulated cervical vertebrae are preserved that likely represent C4, C7 and C8. The cervical vertebrae of *Panphagia* are slightly more elongate than those of *Eoraptor*, the neural arches being proportionately lower. The centra are parallelogram-shaped in lateral view. Their ventral and lateral sides are concave and a keel is present ventrally as in *Eoraptor*.*Panphagia* has two accessory lateroventral ridges on the anterior part of the centrum that converge posteriorly (Figure 6A). The parapophyses are located on the anterior border of the centrum. All preserved cervical vertebrae bear oval scars on the lateral surface at the posterior border of the centra (Figure 6B), a unique character for this taxon. Pleurocoels are absent as in *Eoraptor*. The neural arches are characterized by low neural spines with a convex dorsal border and a prominent, acute anterior corner. The prezygapophyses extend anteriorly farther than in *Eoraptor*. As in sauropodomorphs, the epipophyses do not extend beyond the posterior end of the postzygapophyses, unlike *Eoraptor*, *Herrerasaurus*, and neotheropods such as *Syntarsus*. The presumptive C4 has a distinct prominence located on the neural arch posterodorsal to the diapophysis (Figure 6B), which is not present in *Eoraptor* or any other basal dinosaur. The left prezygapophysis of the presumptive C7 has an abnormal bone growth that has doubled its width compared to its opposite (Figure 6C).

The cervical ribs are gracile with a long rod-shaped shaft directed posteriorly and a delicate anterior process that greatly exceeds the anterior border of the centrum as in *Eoraptor* and most saurischians. The medial surface of the cervical ribs has a deep concavity posterior to the capitulum. The tuberculum is subcylindrical and posterodorsomedially oriented. The broad
capitulum is located on the medial surface of the rib and projects medially toward the parapophysis.

One centrum and four neural arches are preserved from the dorsal column of Panphagia. The centrum belongs to a posterior dorsal vertebra and is similar to that of Eoraptor, although slightly less excavated laterally. The neural arches are have well-developed laminae (prezygodiapophyseal, postzygodiapophyseal, anterior centroparapophyseal, paradiapophyseal and posterior centrodia-pophyseal) that delimit deep infradiapophyseal fossae (Figure 6D). The hyposphene is dorsoventrally short, and the hypantrum is poorly developed (Figure 6E). This is similar to PVSJ 745, and Guaibasaurus [35] but unlike the well developed hypantrum of Herrerasaurus [36], Dilophosaurus [37] and Massospondylus [38], among others.

The preserved anterior (or mid) dorsal rib has a long, robust capitulum and a short, more gracile tuberculum. The capitular articular surface is larger than the tubercular surface. A small lamina spans the distance between both articular facets. The rib curves slightly distal to the union of the capitulum and tuberculum and is straight in anterior view. The posteriorly-bowed shaft has a longitudinal sulcus on its posterodorsal side that vanishes distally.

The only one sacral vertebra preserved, the first primordial sacral. The anteriorly offset, distally expanding rib is C-shaped in lateral view (Figure 6F). The posterior part of the transverse process does not reach the iliac blade (Figure 6G), as in Eoraptor, Saturnalia, Efraasia [39,40], the basal sauropodomorph YPM 56733 [41], and Plateosaurus [42] but unlike Herrerasaurus and neotheropods [42]. As in the cervical series, the caudal vertebrae of Panphagia are proportionally longer and lower than in Eoraptor. The anterior transverse processes are distally expanded as in Eoraptor, but are posterolaterally oriented, instead of laterally as in Eoraptor. The prezygapophyses of the distal caudals are short (Figure 6H), unlike the condition in Herrerasaurus and neotheropods [36]. The hemal arches of the anterior vertebrae are long as in Eoraptor. The lateral surface of the posterior vertebrae presents a longitudinal ridge extending along the centrum just below the neurocentral suture.

Appendicular Skeleton. The scapula of Panphagia is broad and robust (Figure 7). As in Eoraptor [13] and Saturnalia [43], the proximal one-half expands gradually from the neck to the oblique dorsal borders of the acromion and glenoid. This is less derived than the abrupt right angle between the acromion and scapular blade in Herrerasaurus. The scapular blade is strongly expanded distally, the distal end nearly three times broader anteroposteriorly than the neck. This marked distal expansion is greater than that among other basal dinosaurs, which exhibit dital ratios of approximately two (Saturnalia, Eoraptor, Guaibasaurus [44]) or less.

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than two (Asylosaurus [41], Efraasia [45]). The distal border of the blade is canted anteroventrally as in Saturnalia, Guaibasaurus, Syntarsus [25]. In Eoraptor, Asylosaurus, and Herrerasaurus [46], in contrast, the distal end is perpendicular to the long axis of the blade. The posterodorsal corner of the blade has a subtriangular extension (Figure 7A).

The ilium is long and low with a well developed brevis fossa and supraacetabular crest, as in the basal saurischians Eoraptor, Guaibasaurus, and Saturnalia (Figure 8A). The end of postacetabular process bears a shallow depression ventral to the dorsal border; similar scars are present in some basal sauropodomorphs, such as the Mogna specimen (PVSJ 569 [47]). Although located in the same position, this scar differs from the prominent rugosity of Saturnalia [42] and PVSJ 845 [16]. The acetabulum is partially closed as in the basal saurischians Guaibasaurus and Saturnalia. The dorsal border of the pubis seems to be elongated as in most dinosaurs, differing from the short pubis of the basal dinosauromorphs Lagerpeton and Marasuchus [48,2] (Figure 8D–F). The pubic apron is blade-shaped with subparallel lateral and medial margins as in Eoraptor and most sauropodomorphs (Figure 8D). The pubic apron of Panphagia is anteroposteriorly straight as in Saturnalia and differing from the slightly curved pubis of Eoraptor (Figure 8E).

The ischium is long and gracile with a medial lamina restricted to its proximal one-third as in Eoraptor (Figure 8F). Nevertheless, Panphagia has a semicircular section at mid-shaft, unlike the triangular midshaft section of Saturnalia and Eoraptor. The distal end is dorsally expanded as in Saturnalia [42], differing from the slightly expanded distal end of Eoraptor and Herrerasaurus. In distal view the distal end presents a slightly curved pubis of Eoraptor (Figure 8F). The ischium is long and gracile with a medial lamina restricted to its proximal one-third as in Eoraptor (Figure 8F). Nevertheless, Panphagia has a semicircular section at mid-shaft, unlike the triangular midshaft section of Saturnalia and Eoraptor. The distal end is dorsally expanded as in Saturnalia [42], differing from the slightly expanded distal end of Eoraptor and Herrerasaurus. In distal view the distal end presents a slightly curved pubis of Eoraptor (Figure 8E).

The tibia is similar to that of other basal saurischians such as Eoraptor, Herrerasaurus, and Saturnalia. The proximal end is view, differing from the straight border in Saturnalia. The posterior border of the postacetabular process is slightly convex in dorsal view, similar to that in Guaibasaurus and differing from the concave margin that characterizes Eoraptor and Saturnalia.

Although the proximal and distal ends are lacking, the pubis seems to be elongated as in most dinosaurs, differing from the short pubis of the basal dinosauromorphs Lagerpeton and Marasuchus [48,2] (Figure 8D–F). The pubic apron is blade-shaped with subparallel lateral and medial margins as in Eoraptor and most sauropodomorphs (Figure 8D). The pubic apron of Panphagia is anteroposteriorly straight as in Saturnalia and differing from the slightly curved pubis of Eoraptor (Figure 8E).

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The tibia is similar to that of other basal saurischians such as Eoraptor, Herrerasaurus, and Saturnalia. The proximal end is
subtriangular, the cnemial crest projects slightly anteriorly, and the distal end has a short posterolateral process (Figure 9A). The lateral condyle is located close to the posterior border in lateral view, similar to that in *Eoraptor* but differing from the more centered condyle of *Saturnalia*, PVSJ 845 [16], and more advanced sauropodomorphs. The descriptive terms used to differentiate these shapes in lateral view, however, are poorly differentiated. The distal end is subrectangular with the transverse width slightly greater than its anteroposterior length (Figure 9B). This condition is more strongly expressed in more advanced sauropodomorphs, such as *Massospondylus* [38], *Plateosaurus* [49], *Riojasaurus* [50] and others. As in *Saturnalia*, the anteroposterior length of the distal end of the tibia is greater medially than laterally, and the posterior border is slightly concave in distal view. This latter condition is similar to that in *Plateosaurus* but different from the straight or slightly convex border in *Eoraptor* and *Herrerasaurus*. The medial tip of the posterolateral process is distally short (Figure 9C), as in *Eoraptor*, and unlike the distally projected process of *Saturnalia*, *Herrerasaurus*, basal sauropodomorphs and basal neotheropods as *Syntarsus* [32].

The astragalus is subrectangular in proximal view, although the anteromedial corner is particularly prominent (Figure 9D). This condition resembles that in *Saturnalia* but differs from the more rounded anteromedial corner in *Eoraptor*. Although the ascending process is broken, the base is subrectangular and broader laterally than medially with the long axis anteroposteriorly oriented as in *Eoraptor* and *Saturnalia*. The fibular facet is transversally narrow as in *Eoraptor*, *Saturnalia*, and other sauropodomorphs. The elliptical fossa located behind the ascending process is well delimited by a ridge as in *Eoraptor*, *Saturnalia* and other basal sauropodomorphs.

Metatarsal 3 is 50% of the length of the tibia, similar to that in *Eoraptor* and *Herrerasaurus* [36]. The proximal end has a parallelogram shape in proximal view with a uniform transverse width (Figure 9F). This shape is similar to that in *Herrerasaurus* and *Eoraptor* but differs from the subtriangular shape of *Saturnalia* and other basal sauropodomorphs. The shaft is gently bowed medially (Figure 9E). The distal condyles are asymmetrical, the lateral condyle protruding laterally with a deeper extensor pit and collateral ligament fossa.
The three non-ungual pedal phalanges of uncertain position are preserved. These may well be penultimate, or at least distal, because of the presence of well developed posteroventral processes. All have deep extensor and collateral pits, and asymmetrical condyles, resembling those of Eoraptor. The preserved pedal ungual phalanx is gently curved, and presumably belong to digit III, judging for its size and the symmetrical lateral grooves.

Discussion

Comparative Considerations

Panphagia protos exhibits features that place it among dinosaurs, such as a wide transverse fossa on the frontal, reduction of the external mandibular fenestrae; epipophyses on postaxial cervical vertebrae, first sacral rib anteriorly expanded, and well developed brevis fossa on the ilium. It exhibits notable saurischian characters as well, such as the long mid-cervical ribs that are subparallel to the neck, a hypophyseal-hypantrum articulation in the dorsal vertebrae, enlarged sacral transverse processes, a broad supracapsular articular surface of the dentary, lengthening of cervical vertebrae, pubic rudimentary lateral ridge below the tooth row on the lateral view, sublanceolate teeth with lateral prominences on the crowns, dorsoventral compression of the anterior part of the external mandibular fenestra; transverse process of the first primordial sacral vertebra not reaching the ilium, pubic apron blade-shaped with a subparallel lateral and medial margins; distal end of the tibia subrectangular with transverse width slightly greater than the anteroposterior length, medial tip of the posteroventral process of the tibia not distally projected, fibular facet of the astragalus transversely narrow; and ascending process of the astragalus subrectangular with the longer axis anteroposteriorly oriented and laterally wider than medially, among others.

The shared landmarks with Saturnalia are not surprising, because Saturnalia is currently recognized as a sauropodomorph, but the resemblance with Eoraptor is noticeable, especially if it is considered as a theropod [13]. Although the problem of the phylogenetic position of Eoraptor exceeds the purpose of this study, as was noted before, Eoraptor exhibits some features that resemble sauropodomorphs. Those characters are: lanceolate teeth; enlarged external nares; and mandibular joint well below the tooth row [19]. In addition several other characters can be cited: ventral ramus of the squamosal more than five times longer than anteroposteriorly wide; transverse process of the first primordial sacral vertebra not reaching the ilium; reduced olecranon on the ulna; short and pointed preacetabular process; fibular facet of the astragalus transversely narrow; ascending process of the astragalus anteroposteriorly wide; and anteroposterior length of the medial border of the astragalus in proximal view notably wider than that of the lateral border. Moreover, some of the “theropod” characters of Eoraptor, such as the extremely hollow limb bones are also present in basal sauropodomorphs (e.g., Mogosa specimen PVJS 610; BRMSG Ca7456 [24]), suggesting this is a plesiomorphic condition for Saurischia.

Phylogenetic Position

In order to determine the phylogenetic position of Panphagia protos within basal Dinosauria, we decided to add Panphagia to the data matrix published by Langer and Benton [19], because it is a recent study that includes both Saturnalia and Eoraptor. To that analysis we added a line of character states for Panphagia (Table 3).

We maintained the original character states for all the taxa except Eoraptor, for which we corrected several character state scores (Table 3).

We swapped “Other Ornithischia” and “Other Sauropodomorpha” for of “Ornithischians” and “Sauropodomorpha,” respectively, following the phylogenetic definitions for these taxa proposed by Sereno (2005). The new analysis resulted in three

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<th>Table 3. Character state scores for Panphagia protos (PVJS 874) and Eoraptor lunensis (PVJS 512).</th>
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<td>Panphagia ???? ???? ???? ???? 11010 20117 71107 71107 00107 ??</td>
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<td>Eoraptor 01110 11111 11170 17070 71000 10077 71110 71107 01110 ??</td>
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<td>02717 00117 11011 01027 11110 00010 01111 11001 01710 7001</td>
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Data lines inserted into the data matrix of Langer and Benton [19].

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most-parsimonious trees of 187 steps (consistency index 0.561, retention index 0.568) (Figure 10). An implicit enumeration search [52] and jackknifing (probability of character removal 0.36, 1000 resampled matrices) were performed.

All of the most-parsimonious trees nested Panphagia within Sauropodomorpha as the most basal sauropodomorph and sister group to Saturnalia and other sauropodomorphs. These trees differ from those of Langer and Benton [19] in the unresolved position of Silesaurus and Guaibasaurus (Figure 10).

Four synapomorphies unite Panphagia with Saturnalia and other sauropodomorphs: dentary tooth crowns constricted at the base (character 24); lanceolate crowns in most dentary teeth (char. 26); tooth crowns of the anterior quarter of the dentary series higher than the others (character 28); and short posterolateral flange of distal tibia (character 90). The characters that place Panphagia as less derived than Saturnalia are: posteriorly curved crowns (character 25); roughly semicircular distal outline of ischium (character 81); and lateral condyle of tibia posteriorly located (character 85). The aforementioned discussion suggests that Panphagia represents a new distinctive sauropodomorph, representing the most primitive known taxon of Sauropodomorpha.

Early Origin of Sauropodomorpha

The early evolution of saurischians dinosaurs from a small cursorial ancestor [13,19] seems to be confirmed by the recent discoveries of new basal dinosaurs. With the exception of the Herrerasauridae, all of these basal forms are small-bodied species less than 3 m in length, such as Eoraptor, Saturnalia and Guaibasaurus. Panphagia and two new but unpublished basal saurischians from the Carnian Ischigualasto Formation [15,16] are also small-bodied species. The general similarity among all of these basal dinosaurs suggest that few structural changes stand between Eoraptor, Panphagia and the new basal theropod PVSJ 560 [15]. Size increase does not appear to have been a major factor during Carnian times in this region of Pangaea.

The basal sauropodomorph Saturnalia was discovered in the rynchosaur biozone of the Carnian Santa Maria Formation in Brazil, strata widely regarded as contemporary to the Ischigualasto Formation in Argentina based on faunal similarities [53,54]. The absolute age of 228 My (earliest Carnian) for a level 20 meters above the base of the Ischigualasto Formation [7] suggests that deposition of the formation may have begun during the Ladinian. The presence of Panphagia near the base of the Ischigualasto Formation suggests that the origin of Sauropodomorpha occurred during the Ladinian or earlier during the Middle Triassic. Panphagia lived with at least other five different basal dinosaurs (Eoraptor, Herrerasaurus, PVSJ 605 [14], PVSJ 560 [15], and PVSJ 845 [16]) in the lower section of the Ischigualasto Formation, suggesting that saurischian dinosaurs were already well diversified at the dawn of the Carnian.

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Author Contributions

Wrote the paper: RNM OAA.
References


