

VAHINY DEPERETI, GEN. ET SP. NOV., A NEW TITANOSAUR (DINOSAURIA, SAUROPODA)
FROM THE UPPER CRETACEOUS MAEVARANO FORMATION, MADAGASCAR

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ABSTRACT—Here we describe *Vahiny depereti*, gen. et sp. nov., a new titanosaur dinosaur from the Upper Cretaceous Maevarano Formation of northwestern Madagascar. *Vahiny* is distinguished from other titanosaurs by characteristics of the basal tubera, basiptyergoid processes, parasphenoid, and cranial nerve foramina. Diagnostic cranial material of *Vahiny* formalizes the long-standing hypothesis that two titanosaur genera were present in the Late Cretaceous of Madagascar. The other titanosaur, *Rapetosaurus krausei*, is the most common dinosaur in the fauna and is known from hundreds of bones, including multiple partial skeletons and skulls. In contrast, non-*Rapetosaurus* elements are extremely rare. Of these elements, which have been called ‘Malagasy Taxon B,’ we identify a partial braincase as the holotype of *Vahiny depereti*. Although *Vahiny* and *Rapetosaurus* coexisted on the island of Madagascar, differences in their braincases indicate that they are not closely related to one another. Instead, *Vahiny* is most similar to *Jainosaurus* from the Late Cretaceous of India, and shares similarities with the South American taxa *Muyelensaurus* and *Pitekunsaurus*.

INTRODUCTION

Titanosaurs were first recognized in Upper Cretaceous strata from the Mahajanga Basin of northwestern Madagascar by Depéret (1896a, 1896b), less than 20 years after the first descriptions of titanosaurs in India and Patagonia (Lydekker, 1877, 1879, 1893). Since then, continued exploration of the Maastrichtian Maevarano Formation of the Mahajanga Basin (1993–present) has yielded associated and articulated titanosaur skeletons that resulted in the designation of a new taxon, *Rapetosaurus krausei* (Curry Rogers and Forster, 2001, 2004; Curry Rogers, 2009). *Rapetosaurus* is among the most abundant vertebrates of the Maevarano Formation. It is known from a wealth of well-preserved cranial and postcranial remains representing a variety of ontogenetic stages (e.g., Curry Rogers and Forster 2004; Curry Rogers, 2009; Curry Rogers et al., 2011) and has proven pivotal to ongoing revisions of titanosaur anatomy and phylogeny (e.g., Upchurch et al., 2004; Curry Rogers, 2005; Wilson, 2005a; Gallina and Apesteguía, 2011), as well as understanding the distribution and function of titanosaur osteoderms (D’Emic et al., 2009; Curry Rogers et al., 2011).

Throughout the extensive history of paleontological collecting in the Mahajanga Basin, hints of isolated, elongated, and dorsoventrally compressed caudal centra have persistently suggested that more than one titanosaur species may have populated the Maevarano Formation ecosystem (Thevenin, 1907; Huene, 1929; Curry Rogers and Forster, 2001, 2004; Curry Rogers, 2002, 2005; Wilson and Upchurch, 2003). Although clearly distinct from *Rapetosaurus* (e.g., Curry Rogers and Imker, 2007; McNulty et al., 2010), the scattered occurrence and lack of association among these unusual elements prohibited a unified view or definitive diagnosis of ‘Malagasy Taxon B’ (Curry Rogers, 2002, 2005, 2009).

Here we describe *Vahiny depereti*, gen. et sp. nov., a second titanosaur species from the Maevarano Formation. A recently recovered braincase serves as the holotype for this new taxon, which ensures that the name-bearing material of the second Malagasy taxon is stable, particularly because both *Rapetosaurus* and *Vahiny* are known from well-preserved and autapomorphic cranial material. At present, we choose not to assign the fossils previously ascribed to ‘Malagasy Taxon B’ (e.g., flattened caudal vertebrae) to *Vahiny* because field work in the Mahajanga Basin is ongoing, and future discoveries may better resolve associations. Our conservative taxonomic assignment provides a basis for establishing these future associations between *Vahiny*, *Rapetosaurus*, and the as yet undesignated materials in the sauropod collection from the Mahajanga Basin.

Institutional Abbreviations—**FMNH PR**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **ISI**, Indian Statistical Institute, Kolkata, India; **MACN**, Museo Argentino Ciencias Naturales, Buenos Aires, Argentina; **MAU**, Museo Municipal ‘Argentina Urquiza,’ Rincón de los Sauces, Argentina; **PIN**, Russian Academy of Sciences, Moscow, Russia; **PVL**, Fundacion Miguel Lillo, Universidad Nacional de Tucuman, San Miguel de Tucuman, Argentina; **SAM**, Iziko South African Museum, Cape Town, South Africa; **UA**, Université d’Antananarivo, Antananarivo, Madagascar; **UCB**, Université Claude Bernard, Lyon, France; **ZPAL**, Instytut of Paleobiologii, Polish Academy of Sciences, Warsaw, Poland.

SYSTEMATIC PALEONTOLOGY

SAUROPODA Marsh, 1878
NEOSAUROPODA Bonaparte, 1986
TITANOSAURIA Bonaparte and Coria, 1993
VAHINY DEPERETI, gen. et sp. nov.
(Figs. 1–4, 6)

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Etymology—*Vahiny* (Malagasy, pronounced 'va-heenh'), meaning traveler or visitor, reflecting the rarity of this taxon in the Mahajanga Basin. The specific name honors Charles Depéret, who described the original dinosaur material from Madagascar and presciently recognized the sauropod nature of the Malagasy osteoderms.

Holotype—UA 9940, a partial braincase including a partial supraoccipital, basioccipital, basisphenoid, right and left exoccipital-opisthotics, prootics, laterosphenoids, and orbitosphenoids.

Locality and Horizon—MAD 96-07, which is located at coordinates 15°54'56.4"S, 46°35'43.1"E, Berivotra, Mahajanga Basin, northwestern Madagascar. The sediments correspond to Facies 2 of the Maastrichtian-aged Anembalemba Member of the Maevarano Formation (Rogers et al., 2000; Rogers, 2005). The holotypic braincase was found in association with an assortment of Maevarano Formation vertebrates in a time-averaged assemblage, like those preserved at other Maevarano Formation fossil localities (e.g., Rogers et al., 2000, 2007; Rogers, 2005). Fragmentary titanosaur, crocodile, theropod, and turtle limb bones, as well as turtle carapace and plastron, crocodile osteoderms, and theropod teeth were also recovered from surface collection at the site.

Diagnosis—*Vahiny depereti* can be distinguished as a derived member of Titanosauria on the basis of a contact between the quadrate and basal tubera (Wilson, 2002, 2005a). *Vahiny* shares more specific characteristics with the Indian titanosaur *Jainosaurus* and with South American titanosaurs *Muyelensaurus* (Calvo et al., 2007) and *Pitekunsaurus* (Filippi and Garrido, 2008). These include the presence of a broad, shallow fossa between the basal tubera, basiptyergoid processes that are oriented parallel to the occipital plane, and a long prootic spur that extends onto the basiptyergoid process. *Vahiny* and *Muyelensaurus* (Calvo et al., 2007) also share basiptyergoid processes that diverge via a broad, 'U'-shaped embayment. *Vahiny* and *Jainosaurus* share basal tubera that exhibit a small ventrolateral process set off by a notch that is continued by an elongate groove (Wilson et al., 2009). *Vahiny depereti* is characterized by the following autapomorphies: basal tubera that are composed mainly of the basioccipital, with a reduced contribution from the basisphenoid; a thick web of bone separating the basiptyergoid embayment from the basal tubera, visible posteriorly; paired blind fossae present between the basiptyergoid processes and parasphenoid rostrum; ventrally keeled and dorsally troughed parasphenoid rostrum; and foramina for cranial nerves V, III, and II are co-linear, and the metotic foramen is displaced ventrally from them.

Referred Material—FMNH PR 3046, an isolated juvenile basioccipital (Fig. 5) recovered from Facies 1 of the Anembalemba Member of the Maevarano Formation at locality MAD 93-18, Berivotra, Madagascar.

DESCRIPTION

Below we describe the holotypic *Vahiny* braincase as well as a referred juvenile basioccipital. The descriptions and comparisons that follow are based upon study of collections of Malagasy dinosaurs held at the Université d'Antananarivo, Stony Brook University, and the Field Museum of Natural History. Unless otherwise stated, descriptions are based primarily upon the holotypic braincase. Additional insights were gleaned from titanosaurs housed in collections in India, Argentina, Brazil, and France, and descriptions available in the published literature. We employ traditional orientational descriptors (e.g., anterior, posterior) rather than the standardized terms (i.e., cranial, caudal) applied to mammals and birds (see Wilson, 2006). We refer to cranial nerve foramina by their number (e.g., foramen for cranial nerve V) rather than their common name (i.e., trigeminal foramen).

We describe the median and paired paramedian bones that form the floor, posterior wall, and lateral walls of the braincase, drawing attention to connections between bones as well as the foramina passing through or between them. We designate the surface of the occiput as a vertical reference plane that can be used to measure angular orientation of projecting structures (e.g., basiptyergoid processes) for comparative purposes (see Wilson et al., 2009:25, 34). Principal dimensions of the holotypic braincase and referred basioccipital are provided in Table 1.

Preservation

The holotypic braincase lacks the distal ends of the paroccipital processes, basiptyergoid processes, and parasphenoid rostrum. Most of the supraoccipital and the dorsal margins of the laterosphenoid and orbitosphenoid have been broken away. The frontals and parietals were not preserved, which permits a view into the endocranial cavity and hypophyseal fossa. Openings for cranial nerves I–XII are preserved on one or both sides of the skull (Figs. 1–4).

Supraoccipital

The supraoccipital forms the posterodorsal part of the braincase, contacting the parietal anterodorsally and the exoccipital-opisthotic ventrolaterally. The supraoccipital is poorly preserved in the holotypic braincase; thus, many critical features cannot be observed (e.g., nuchal crest).

Sutures between the exoccipital-opisthotics and supraoccipital are completely fused, but low, transversely oriented ridges at the dorsal margin of the foramen magnum probably mark the medial-most part of their course. If these indeed represent part of the suture between the supraoccipital and exoccipital-opisthotic, the supraoccipital probably had at least a small contribution to the foramen magnum. The central portion of the nuchal crest is not preserved in *Vahiny*, but low, paramedian prominences mark its ventrolateral margins. These ridges are more laterally positioned and narrower than the paramedian, more vertically oriented ridges observed in *Rapetosaurus*. Due to incomplete preservation of the supraoccipital, neither its height relative to the foramen magnum nor the form of its nuchal crest are known.

Basioccipital

The basioccipital is the posterior-most ventral median braincase element. It is completely preserved and forms most of the occipital condyle and basal tubera.

The occipital condyle projects ca. 90° from the occipital plane and is subparallel with the estimated orientation of the skull roof (Figs. 1–3). As in *Jainosaurus* (Wilson et al., 2009; Fig. 6A, E), the articular surface of the occipital condyle extends ventrally, suggesting either the skull was deflected slightly ventrally relative to the vertebral axis or that the atlantal articular surface extended ca. 1.5 cm farther anteriorly than did the odontoid. The absence of sutures makes it difficult to discern the relative contribution of the exoccipital-opisthotic to the occipital condyle in the holotypic braincase, but it clearly contributed at least the dorsolateral shoulders of the condyle, because the exit for cranial nerve XII is partly preserved on its neck. In *Rapetosaurus*, for example, this opening is completely enclosed by the base of the exoccipital-opisthotic (Curry Rogers and Forster, 2004:fig. 19). The referred juvenile basioccipital, which is not fused to the exoccipital-opisthotic, exhibits strongly beveled sutural facets that nearly meet on the midline, leaving only a median sliver of basioccipital at the floor of the foramen magnum (Fig. 5A, D). This indicates a substantial contribution of the exoccipital-opisthotic to the occipital condyle at least early in ontogeny. *Vahiny* lacks the small, ventrally facing depression between the occipital condyle and basal tubera that is observed in

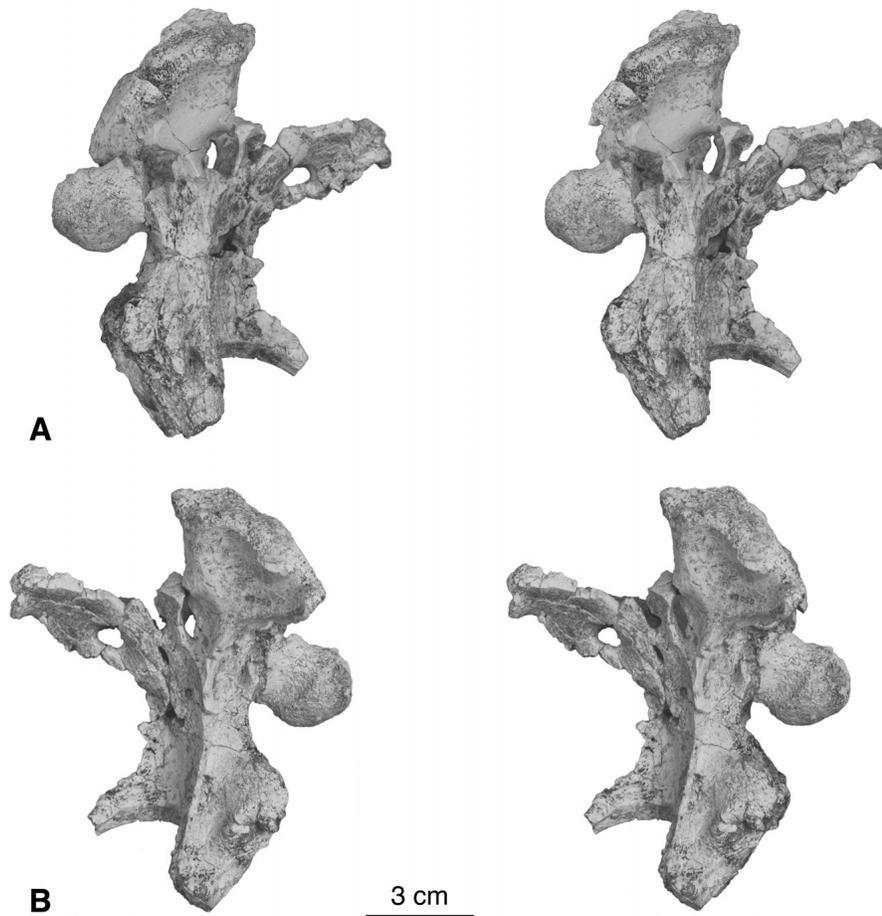


FIGURE 1. *Vahiny depereti*, holotypic braincase (UA 9940). Stereopairs in **A**, right lateral view; **B**, left lateral view. Scale bar equals 3 cm.

Jainosaurus, *Rapetosaurus*, and some other neosauropods (Wilson et al., 2009). The metotic foramen (for cranial nerves IX–XI and the jugular vein) and foramen ovale (cranial nerve VIII) occur at the intersection between the basioccipital, basisphenoid, exoccipital-opisthotic, and prootic.

The basal tubera are anteroposteriorly thin, sheet-like structures, as they are in *Saltasaurus* (Wilson, 2002) and certain other titanosaurs. The basal tubera appear to be primarily composed of the basioccipital, with a smaller, possibly negligible contribution from the basisphenoid. This is especially apparent in the juvenile, unfused basioccipital, in which the basal tubera bear smooth distal surfaces that lack articular facets for the basisphenoid (Fig. 5E). In posterior view, the basal tubera form a trapezoid whose upper base is ca. 3 cm and whose lower base is 5 cm. The symmetrical legs of the trapezoid diverge ventrally to become much broader transversely than is the occipital condyle. The basal tubera are concave dorsoventrally and transversely, as in *Jainosaurus* and the South American titanosaurs *Muyelensaurus*, *Pitekunsaurus*, and MML 194 (see Wilson et al., 2009; Figs. 2D, 3B; Table 1). In lateral view, the basal tubera extend posteriorly as far as the occipital condyle (Figs. 1–3). The basal tubera are ventrolaterally thickened and roughened, which may indicate a bony connection between the basal tubera and the medial aspect of the quadrate. A small, lateral, pendant process is sharply divided from the rest of the basal tubera by a deep notch (Figs. 2C, 3B, 5B, D). Just ventral to this notch is a conspicuous groove that extends to the preserved end of the basiptyergoid

processes. The ventrolateral notch and processes are incipiently developed in the referred juvenile basioccipital (Fig. 5D), and all three features are well developed in *Jainosaurus* (Wilson et al., 2009), which indicates their close common ancestry.

The basioccipital-basisphenoid suture is fused in the holotypic specimen, but a well-defined ridge may approximate its position (Figs. 1, 2D, 3). The sutural contact between these two

TABLE 1. Principal dimensions (in mm) of the braincase of *Vahiny depereti*.

| Region | Dimension | Holotype (UA 9940) | Referred (FMNH PR 3046) | |
|-------------------------|--------------------------------|--------------------|-------------------------|------|
| Lateral skull | Length | 99.4* | — | |
| | Occipital condyle | Width | 29.4 | 16.6 |
| | | Height | 24.0 | 14.3 |
| Foramen magnum | Length | 30.0 | — | |
| | Width | 18.3* | — | |
| | Height | 24.9* | — | |
| Basal tubera | Width | 62.4 | 11.7 | |
| Basiptyergoid processes | Length, distal to basal tubera | 25.0* | — | |
| Hypophyseal fossa | Width | 16.9 | — | |
| | Length | 7.9 | — | |

Asterisks (*) indicate measurement of an incomplete structure.

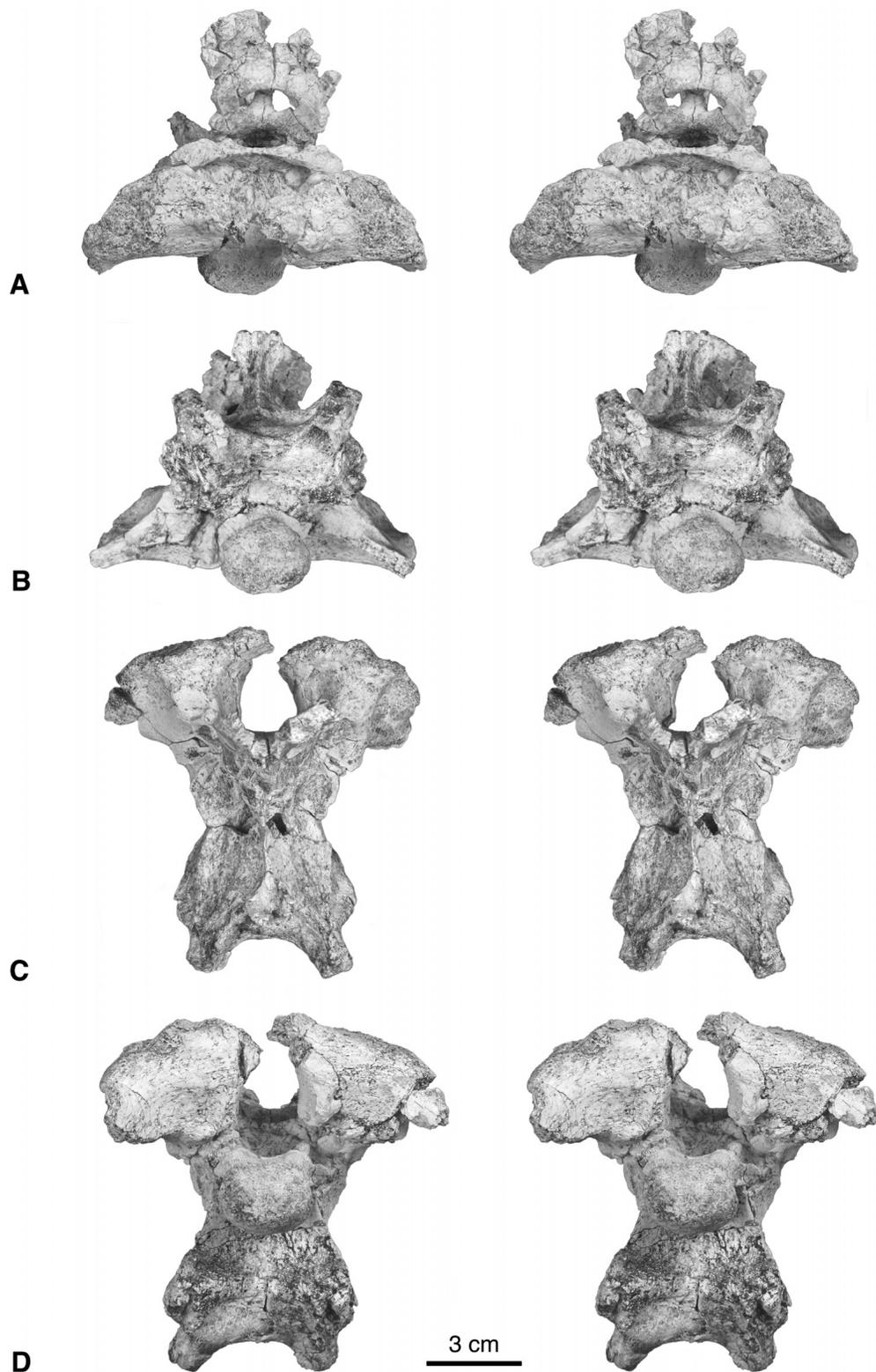


FIGURE 2. *Vahiny depereti*, holotypic braincase (UA 9940). Stereopairs in **A**, dorsal view; **B**, ventral view; **C**, anterior view; and **D**, posterior view. Scale bar equals 3 cm.

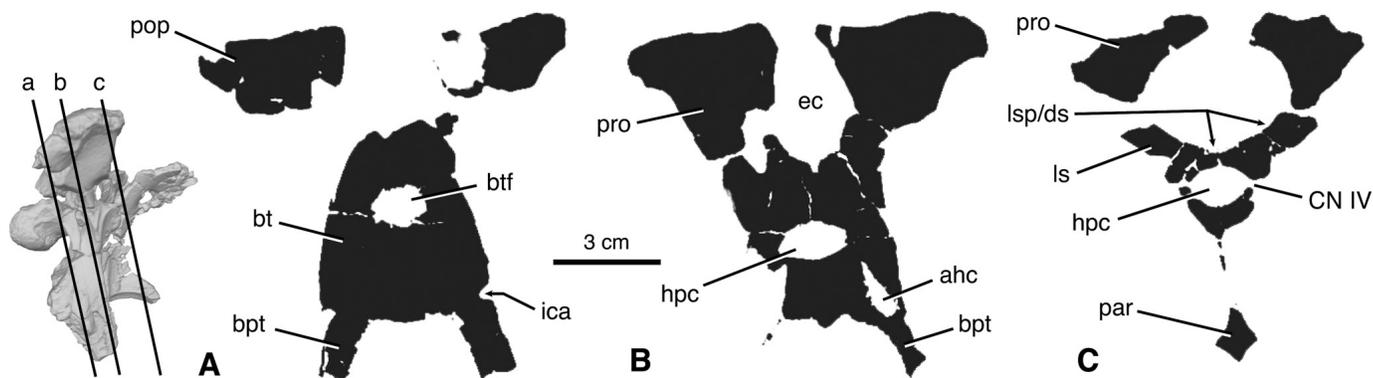


FIGURE 4. *Vahiny depereti*, holotypic braincase (UA 9940). Three transverse CT sections passing through the braincase at the approximate positions shown in the surface-rendered braincase at left (a–c). The section shown in **A** is at level of internal carotid foramen; section in **B** is at level of adenohypophyseal canal; section in **C** is at level of parasphenoid rostrum. **Abbreviations:** ahc, adenohypophyseal canal; bpt, basipterygoid process of basisphenoid; bt, basal tubera; btf, basal tubera fossa; CN IV, foramen for cranial nerve IV; ds dorsum sellae; ec, endocranial cavity; hpc, hypophyseal canal; ica, foramen for the internal carotid artery; ls, laterosphenoid; lsp, laterosphenoid pillar; par, parasphenoid rostrum; pop, paroccipital process; pro, prootic. Scale bar equals 3 cm.

dermal parasphenoid bone as it does in squamates and other reptiles (e.g., Zaher et al., 2009). Most sauropod braincase descriptions, however, use the term basisphenoid (e.g., Paulina Carabajal, 2012), and we retain that term here without implying a separate parasphenoid bone.

A conspicuous ridge, the dorsum sellae, crosses the floor of the endocranial cavity just posterior to the hypophyseal fossa, near the junction of the basisphenoid, prootic, and laterosphenoid (Figs. 2A, 3A). The dorsum sellae is continuous with the laterosphenoid ‘pillars’ (see below), as it is in some titanosaurs (*Rapetosaurus*, Curry Rogers and Forster, 2004; unnamed forms, Paulina Carabajal and Coria, 2007; Garcia et al., 2008). A hint of a suture on the posteroventral margin of the dorsum sellae may indicate the basisphenoid-laterosphenoid contact. Paired openings for cranial nerve VI pierce the braincase floor just posterior to the dorsum sellae and exit ca. 1.5 cm ventral to the line that connects the openings for cranial nerves II, III, and V (Figs. 1, 3C, D). Just posterior to these openings on the floor of the braincase is a median opening that may represent a vascular canal. Just anterior to

the dorsum sellae is the hypophyseal fossa (sella turcica), which is formed by the basisphenoid, laterosphenoids, and orbitosphenoids. The hypophyseal canal expands into a deep fossa that is visible through the broken anterolateral surface of the basisphenoid.

The basipterygoid processes are incomplete distally, but they would have been fairly elongate. The distance from the base of the occipital condyle to the ends of the basal tubera is slightly less than the distance from the ends of the basal tubera to the ends of the preserved basipterygoid processes (Table 1). The left and right basipterygoid processes diverge from the mid-sagittal plane at an angle of approximately 50°, and together they are angled 147° anteriorly relative to the occipital plane (Figs. 1, 2C, D, 3C–D). A broad, ‘U’-shaped embayment separates the basipterygoid processes, as it does in other titanosaurs (e.g., *Muyelensaurus*; Calvo et al., 2007). The embayment extends to within ca. 2 cm of the basal tubera, separated from them by a ribbon of bone that is visible posteriorly (Figs. 2B, 3B). This latter feature may be unique to *Vahiny*.

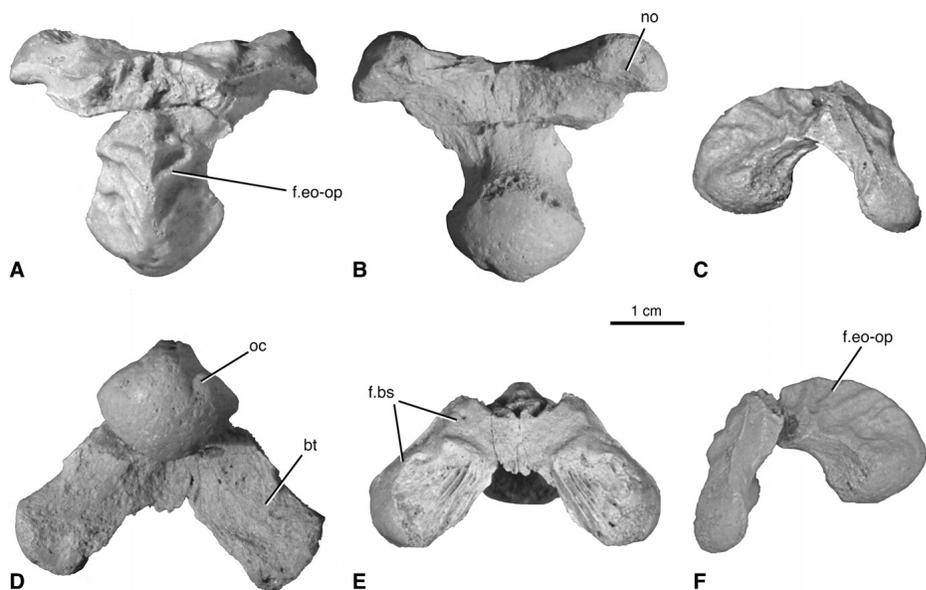


FIGURE 5. *Vahiny depereti*, referred juvenile basioccipital (FMNH PR 3046) in **A**, dorsal view; **B**, ventral view; **C**, right lateral view; **D**, posterior view; **E**, anterior view; **F**, left lateral view. **Abbreviations:** bt, basal tubera; f.bs, facet for basisphenoid; f.eo-op, facet for exoccipital-opisthotic; no, notch at distal end of basal tubera; oc, occipital condyle. Scale bar equals 1 cm.

The long spur of the crista prootica continues onto the basisphenoid as a conspicuous ridge that is visible on the anterolateral edge of the basiptyergoid processes. At the level of the occipital condyle, the crista prootica separates into troughs extending ventrally from the metotic foramen (posteriorly) and the foramen for maxillary and mandibular branches of cranial nerve V (anteriorly). Further ventrally, the continuation of this ridge separates two openings. The more posteriorly positioned of these openings is located near the basioccipital-basisphenoid contact and represents the opening for the internal carotid artery (Fig. 4A). The more anteriorly positioned of these openings passes through the basisphenoid and enters the hypophyseal fossa (Fig. 4B). It may represent a canal into the adeno-hypophysis, as suggested by Paulina Carabajal (2012) for that structure in *Bonaititan*. Computed tomography (CT) scans show that the opening for the internal carotid artery probably met the adeno-hypophyseal canal in the hypophyseal fossa (Fig. 4B). The position of the internal carotid arteries on the lateral aspect of the basiptyergoid processes is common in non-titanosaur sauropods but apparently rare within titanosaurs, in which they open medially, between the basiptyergoid processes (Paulina Carabajal, 2012). There are paramedian depressions located between the basiptyergoid processes in *Vahiny*, but no foramina can be observed, and CT scans reveal that the depressions did extend into the hypophyseal fossa (Fig. 4). Thus, *Vahiny* and *Jainosaurus* share a primitive feature of laterally positioned openings for the internal carotid arteries.

The basiptyergoid processes do not appear to taper anteroposteriorly or transversely. In cross-section, the basiptyergoid processes are anteroposteriorly elongated and elliptical, with a slight concavity on the medial surface. Anteriorly, each crista prootica meets a ridge extending ventrolaterally from the median parasphenoid. In anteroventral view, between the paired ventrolateral parasphenoid ridges, are small fossae that contain foramina that may have transmitted vasculature to the adeno-hypophysis (Paulina Carabajal, 2012), as mentioned above. The presence of these openings in *Jainosaurus* cannot be determined in either of the exemplars, because in both cases that portion of the braincase was not preserved.

The parasphenoid, or cultriform process, lacks only its distal end. It is fairly robust, which contrasts with the transversely thin, sheet-like processes found in some other titanosaurs (e.g., *Rapetosaurus*; Curry Rogers and Forster, 2004). The parasphenoid expands anteriorly to form a robust process that terminates in an anteroventrally directed, distally broadening 'U'-shaped trough (Figs. 1, 2). The ventral surface of the parasphenoid bears a sharp midline ridge with laterally beveled edges. Just posterolateral to this ridge, between the basiptyergoid processes, are two blind depressions that are located where the internal carotid arteries open in some titanosaurs (e.g., *Saltasaurus*).

Exoccipital-opisthotic

The paired exoccipital-opisthotic elements form part of the posterior wall of the endocranial cavity, as well as the paroccipital processes, the lateral margins of the foramen magnum, and the dorsolateral portions of the occipital condyle. The exoccipital-opisthotics are partially preserved, lacking all but the base of the paroccipital processes and missing the ventrolateral border of the foramen magnum (Fig. 2A, B, D). The exoccipital-opisthotic is fused to both the supraoccipital and the basioccipital, but part of its suture with the prootic can be discerned on the left side, in the cross-section through the paroccipital process. Ventrally, between these two bones open the foramina for cranial nerves VII–XI. The paroccipital processes do not exhibit the sharp notch in their narrow dorsal border that characterizes *Jainosaurus* and *Rapetosaurus* (Wilson et al., 2009). Instead, they are anteroposteriorly broad and, where fused

with the prootic, slightly sinuous along the squamosal articular surface.

The exoccipital-opisthotic articulates with the basioccipital via a nearly horizontal suture that begins at the metotic foramen and extends posteriorly onto the occipital condyle. The exoccipital-opisthotics extend medially nearly to the midline, but they do not quite exclude the basioccipital and supraoccipital from the ventral-most and dorsal-most portions of the foramen magnum, respectively. Just lateral to the dorsal-most point of the foramen magnum are two transversely oriented low ridges that mark the part of the contact between the supraoccipital and exoccipital-opisthotic (Fig. 3B). These facets also serve as the point of articulation of the proatlas, which were not preserved with this specimen.

Prootic

The prootic forms the posterior-most lateral wall of the braincase. In the *Vahiny* holotype, the prootic is completely fused to the basisphenoid and nearly completely fused to the exoccipital-opisthotic, with a trace of the suture visible in the paroccipital process. In a subadult specimen of *Rapetosaurus*, a gap in the intersection of these elements forms the metotic foramen (Curry Rogers and Forster, 2004:figs. 23, 24).

The crista prootica is an elongated vertical crest that extends from a position dorsal to the metotic foramen all the way to the anterior border of the basiptyergoid processes. The crista prootica is posteriorly concave and visible in anterior, posterior, and lateral views (Figs. 1, 2C, D, 3). At the level of the occipital condyle, it separates the metotic foramen from the foramen for cranial nerve V. Further ventrally, it separates the foramen for the internal carotid artery and the canal into the adeno-hypophysis.

No semicircular canals are visible in CT images of the holotype, but the broken right prootic preserves a depression that may be the opening into the inner ear.

Laterosphenoid

The laterosphenoid is a transversely oriented element that abuts the prootic posteriorly and is nearly fused to the basisphenoid ventrally and to the orbitosphenoid anteriorly. The pillar-like laterosphenoids extend medially to contact one another on the midline, as indicated by a trace of a suture on the posterior aspect of the dorsum sellae. The dorsal portion of the laterosphenoid (e.g., laterosphenoid head) is not preserved in the holotype. As a consequence, its sutural articulations with the postorbital, frontal, and parietal are unknown. The suture between the laterosphenoid and orbitosphenoid is not preserved, but it was likely positioned near the openings for cranial nerves III and IV, as it is in most other sauropods.

The laterosphenoid forms the crista antotica, which is a ridge that forms the anterior margin of the foramen for cranial nerve V and part of the groove for its maxillary and mandibular branches. The preserved portion of the crista antotica is much lower in relief than the laterosphenoid pillar. This pillar corresponds to the division between the forebrain and midbrain (e.g., Wilson et al., 2009).

Orbitosphenoid

The orbitosphenoids enclose the forebrain anteriorly and form the anterior portion of the hypophyseal fossa. The orbitosphenoid, laterosphenoid, and basisphenoid are completely fused in the holotype (UA 9940). Internally, the optic nerve (cranial nerve II) foramina open within a fossa in the body of the orbitosphenoids. They are directed anteroventrally and divided on the midline by a thin bony isthmus (Figs. 1, 2A, 3C, D). The anterodorsal-most portion of the orbitosphenoid is most completely preserved

on the left side, where it is anteroposteriorly and transversely expanded. The slightly dorsally concave portion of the orbitosphenoid would have formed the lower margin of the foramen for cranial nerve I.

Cranial Nerves

Openings for the anterior cranial nerves are well preserved on both sides of the braincase, and the posterior cranial nerve openings (VII–XII) are partially preserved on at least one side of the holotypic braincase (UA 9940). Openings for cranial nerves II, III, V, and XII and the metotic foramen form a line that extends to the foramen magnum (Figs. 1, 3C, D). Openings for cranial nerves I and IV are positioned dorsal to this line, and the opening for cranial nerve VI is positioned ventral to it, as in other sauropods (Wilson et al., 2009).

The dorsal margin for cranial nerve I, which is normally formed by the skull roof, is not preserved. The ventral border is formed by the conjoined orbitosphenoids. The foramina for cranial nerve II are completely preserved in the holotypic braincase, where they occur within an elevated shelf. It appears that this foramen is mainly composed of the orbitosphenoid, but it may receive a small midline contribution from the parasphenoid. The opening for cranial nerve III is small and occurs anterior to the crista antotica (Fig. 3), dorsal to the hypophyseal fossa. Its borders are formed by the orbitosphenoid anteriorly, the laterosphenoid posteriorly, and the basisphenoid ventrally. The opening for cranial nerve IV also likely occurs along the suture between the laterosphenoid and the orbitosphenoid in a line dorsal to the opening for cranial nerve III (Fig. 3). In *Vahiny*, the opening for cranial nerve IV is broken dorsally, but it is larger than the foramen for cranial nerve III. The foramen for cranial nerve V opens between the laterosphenoid, prootic, and basisphenoid. It is large and probably accommodated all three branches of cranial nerve V. The path of the mandibular branch of the trigeminal nerve is marked by a shallow groove that extends along the anterior surface of the crista prootica. The opening for cranial nerve VI is ventral to these other foramina, on the anterolateral surface of the basisphenoid (Figs. 1–3). It exits slightly below the opening for cranial nerve III. The opening for cranial nerve VII is a tiny, rounded foramen positioned on the posterior surface of the crista prootica. The metotic foramen, which transmitted cranial nerves IX–XI and the jugular vein, and the foramen ovale (cranial nerve VIII) occur in a large fossa posterior to the crista prootica. Although the ventral margins of the fossa are preserved, the other borders of these foramina are not visible. Ventrally directed grooves on the posterior side of the crista prootica and on the basisphenoid indicate the paths of these nerves. A single opening for cranial nerve XII is located on the dorsal surface of the neck of the occipital condyle.

COMPARISONS AND PHYLOGENETIC AFFINITIES

Titanosaur phylogeny remains poorly resolved, despite numerous recent cladistic analyses that have focused on the group (e.g., González Riga, 2003; Curry Rogers, 2005; Calvo et al., 2007; Zaher et al., 2011). Lack of phylogenetic resolution may be due to a combination of interrelated factors that include (1) the nature of the titanosaur body fossil record, which thus far has produced relatively few skulls or articulated skeletons (e.g., Mannion and Upchurch, 2010); (2) undocumented field associations between elements in a type series, which characterizes many early descriptions of titanosaur genera, including '*Titanosaurus madagascariensis*'; (3) the global nature of their fossil record and resultant wide geographic range of collections, which make it difficult to make first-hand observations on many different taxa; (4) genera based on fragmentary remains; and (5) generic

diagnoses based upon features that have obsolesced to describe a broader distribution of titanosaurs. As such, the precise relationships of *Vahiny* and other titanosaurs must await ongoing taxonomic revision of several titanosaur genera and a more comprehensive analysis of titanosaur phylogeny. Here we provide general comparisons to titanosaur taxa that have basicranial material from Cretaceous rocks in Madagascar (*Rapetosaurus*), India (*Jainosaurus*, *Isisaurus*), South America (*Antarctosaurus*, *Saltasaurus*, *Muyelensaurus*, *Pitekunsaurus*, *Bonatitan*), Asia (*Nemegtosaurus*), and Africa (*Malawisaurus*) (Fig. 6).

Rapetosaurus

Two *Rapetosaurus* skulls, as well as abundant isolated cranial material pertaining to juvenile and adult individuals, have been recovered from the Maevarano Formation. The holotypic skull of *Rapetosaurus krausei* (UA 8698) included a partial basioccipital and exoccipital-opisthotic preserving the occipital condyle, right basal tuber, and paroccipital process. The referred juvenile skull (FMNH PR 2192), which was found in association with a postcranial skeleton, is better preserved and includes a fused basioccipital and basisphenoid that articulate with a right exoccipital-opisthotic, supraoccipital, and a left laterosphenoid.

Features of the basicranium clearly distinguish *Rapetosaurus* and *Vahiny*, particularly the morphology of the basal tubera, basiptyergoid processes, and parasphenoid rostrum (Fig. 6A, B). In *Vahiny*, the occipital condyle is a little wider than it is tall, whereas in *Rapetosaurus* the condyle is slightly taller than it is wide. The foramen magnum in *Vahiny* is taller than it is wide, whereas in *Rapetosaurus* these dimensions are equal. The supraoccipital is incompletely preserved in *Vahiny*, but the preserved region appears relatively flat and suggests the presence of a single nuchal crest, which contrasts with the median groove present in the nuchal crest of *Rapetosaurus*.

The basal tubera of *Vahiny* are composed mainly of the basioccipital, with a negligible contribution from the basisphenoid. They are separated by a broad posterior fossa that is not punctuated by vasculature. The basioccipital between the basal tubera is nearly sheet-like, with a straight ventral border that grades smoothly into the anteriorly positioned basisphenoid. This morphology contrasts sharply with that of *Rapetosaurus*, in which the basal tubera are transversely narrow and have equal contributions from the basioccipital and basisphenoid. A deep 'V'-shaped notch separates the basal tubera in *Rapetosaurus*, and there are vascular pits ventral to the occipital condyle and between the basal tubera. Rather than grading gently into the basiptyergoid processes, in *Rapetosaurus* the basal tubera are sharply offset from them (FMNH PR 2192). In *Vahiny*, the basiptyergoid processes are deflected anteriorly relative to the occipital plane and separated by a broad, 'U'-shaped embayment that is wider than the occipital condyle. Although the distal ends of the basiptyergoid processes are not preserved in *Vahiny*, the basisphenoid exposure on the posterior surface of the braincase is far smaller than in *Rapetosaurus*. Similarly, the basiptyergoid processes in *Rapetosaurus* are angled anteriorly relative to the occiput (Curry Rogers and Forster, 2004). The position of the internal carotid arteries also differs in *Rapetosaurus* and *Vahiny*. In *Vahiny*, as in most non-titanosaur sauropods, the foramina for the internal carotids are lateral to the basiptyergoid processes, but in *Rapetosaurus* they are more anteriorly and medially positioned (FMNH PR 2192).

In *Vahiny*, the parasphenoid rostrum is a triangular trough with strongly beveled lateral margins that exhibits ridges and valleys containing vascular foramina. In *Rapetosaurus*, the parasphenoid is sheet-like and lacks foramina or sculpturing.

The foramina for cranial nerves II–V occur at slightly different positions in *Vahiny* and *Rapetosaurus* (FMNH PR 2192). In *Vahiny*, the foramen for cranial nerve IV is positioned slightly

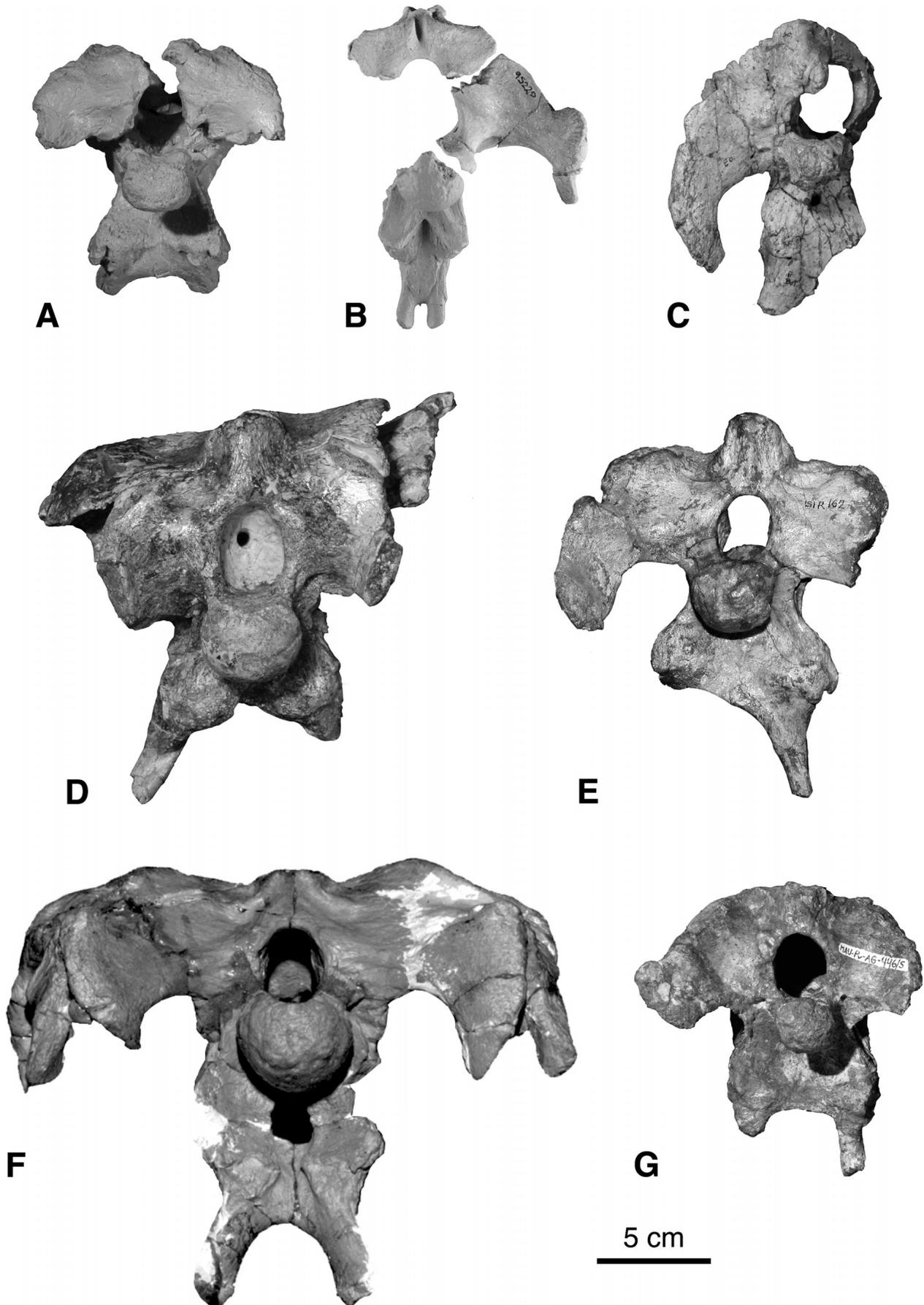


FIGURE 6. Titanosaur basicranial comparisons. **A**, *Vahiny depereti* (UA 9940); **B**, *Rapetosaurus krausei* (FMNH PR 2192); **C**, *Saltasaurus loricatus* (PVL 4017); **D**, *Antarctosaurus wichmannianus* (MACN 6904); **E**, *Jainosaurus septentrionalis* (ISI R 199); **F**, *Quaesitosaurus orientalis* (PIN 3906/2); **G**, *Pitekunsaurus macayai* (MAU-Pv-AG-446). The articulated quadrates and pterygoids were digitally removed from the posterior view of *Quaesitosaurus* for ease of comparison with other braincases (compare with Wilson, 2005b:fig. 18). Scale bar equals 5 cm.

dorsal to a line drawn connecting the ventral margins of the foramina for cranial nerves II and V, whereas the foramen for cranial nerve III is ventral to this line. In *Rapetosaurus*, the foramina for cranial nerves II and V are not in horizontal alignment. Instead, the foramen for cranial nerve V is dorsal to cranial nerve II, and is more aligned with the foramen for cranial nerve IV. Likewise, cranial nerves II and III are in horizontal alignment in *Rapetosaurus* (FMNH PR 2192).

Jainosaurus

The hypodigm of *Jainosaurus septentrionalis* includes two braincases (K27/429, ISI R162) and assorted postcranial elements (Huene and Matley, 1933; Chatterjee and Rudra, 1996; Wilson et al., 2009, 2011). There are a number of similarities between the braincases of *Vahiny* and *Jainosaurus*, which may indicate that their sister-taxon relationship, although this hypothesis remains to be tested in a phylogenetic analysis (Fig. 6A, E). Both *Jainosaurus* (ISI R162) and *Vahiny* possess a small, laterally oriented, pendant process and notch on the basal tubera. In both taxa, this notch extends as a straight groove on the posterolateral aspect of the basiptyergoid process. *Jainosaurus*, *Vahiny*, and certain South American taxa (see below) also share the presence of a broad, shallow fossa between the basal tubera. The basal tubera of *Vahiny* are composed primarily of the basioccipital, whereas in *Jainosaurus* they receive a greater contribution from the basisphenoid (ISI R162). The basiptyergoid processes in *Vahiny* are angled 147° anteriorly relative to the plane formed by the preserved portion of the braincase dorsal to the foramen magnum, in contrast with the basiptyergoid processes of *Jainosaurus*, which are parallel to the occipital plane (Wilson et al., 2009). The basiptyergoid processes of *Vahiny* diverge from the midline via a broad, 'U'-shaped embayment rather than the acute angle seen in *Jainosaurus* (ISI R162; Wilson et al., 2009).

Other Titanosaurs

Isisaurus—The Late Cretaceous Indian titanosaur *Isisaurus* (ISI R199; Berman and Jain, 1982) is distinguished from *Jainosaurus* and *Vahiny* by the strong downward deflection of the occipital condyle. Other distinguishing features include the small, circular proatlantal facets and broad supraoccipital wedge present in *Isisaurus*. Both *Vahiny* and *Jainosaurus* bear weaker proatlantal facets and less prominent supraoccipital wedge.

Muyelensaurus—Calvo et al. (2007:fig. 4) described a braincase of *Muyelensaurus* that, like *Vahiny*, has basal tubera that are joined by a thin, concave lamina that terminates laterally in a sharp ridge. The occipital condyle is wider than the dorsal base of the basal tubera in *Muyelensaurus*, but in *Vahiny* it is slightly wider than the occipital condyle, as it is in many sauropods. Unlike *Muyelensaurus*, *Vahiny* does not exhibit a wide, ventral depression below the basal tubera. The basiptyergoid processes are not preserved in *Muyelensaurus*, but Calvo et al. (2007:489) suggest on the basis of the preserved right basiptyergoid process that they are deeply separated and parallel, not laterally divergent as in *Vahiny*.

Pitekunsaurus—*Vahiny* and *Pitekunsaurus* (Fillipi and Garrido, 2008) share the general features of broadly divergent basal tubera and the 'U'-shaped separation between the elongated basiptyergoid processes. However, they differ in several respects. In *Pitekunsaurus*, the broad fossa dorsal to the basal tubera is proportionately shorter than that in *Vahiny* (Fig. 6A, G). The basiptyergoid processes are directed nearly vertically in *Pitekunsaurus*, as in *Jainosaurus*, whereas they are more anteriorly directed in *Vahiny*. The parasphenoid is slightly more elevated relative to the basal tubera in *Pitekunsaurus* than in *Vahiny*.

Bonatitan—Like *Isisaurus*, *Bonatitan* (Martinelli and Forasiepi, 2004) has a ventrally deflected occipital condyle relative to the occipital plane. This differs from the more

horizontally oriented condyle in *Vahiny*. The basal tubera also differ between these taxa. The basal tubera are fairly heavy and have a stepped margin relative to the basiptyergoid processes in *Bonatitan*, as in *Rapetosaurus*. *Bonatitan* and *Jainosaurus* share the broadly separated, nearly vertically oriented basiptyergoid processes. The endocast of *Bonatitan* has recently been redescribed by Paulina Carabajal (2012), who noted the medial positioning of the foramina for the internal carotid arteries. In addition, *Bonatitan* has an anteriorly deflected occiput in which the occipital fossa on the parietals is angled forward and dorsally.

Antarctosaurus—Like *Bonatitan*, *Antarctosaurus* (MACN 6904; Huene, 1929:pl. 28; Powell, 2003) has a well-marked occipital fossa on the parietal that is expressed as a bulge on the dorsal surface of the skull. The occipital condyle is deflected ventrally, as is the parasphenoid rostrum. The basal tubera are thin and arched posteriorly in *Antarctosaurus*, a feature shared with *Vahiny* (Fig. 6A, D). The internal carotid arteries are located near the midline in *Antarctosaurus* (Paulina Carabajal, 2012) rather than on the lateral aspect of the basiptyergoid process, as they are in *Vahiny*.

Saltasaurus—*Saltasaurus* and *Vahiny* share the broad, concave surface between basal tubera ventral to the occipital condyle, but they differ in the development of the tubera themselves (Fig. 6A, C). In *Vahiny*, the basal tubera are topographically distinctive, whereas in *Saltasaurus* they are relatively flat and flush with the laminar sheet between them (PVL 4017; Powell, 2003). They also differ in the position of the internal carotid arteries, which open between the basiptyergoid processes in *Saltasaurus* but lateral to them in *Vahiny*, as in *Jainosaurus*. The basiptyergoid processes are autapomorphically thin and platy in *Saltasaurus* (PVL 4017), and the occipital condyle is taller and narrower than in *Vahiny*.

Nemegtosaurus* and *Quaesitosaurus—Like *Rapetosaurus*, *Nemegtosaurus* (ZPAL MgD-I19) and *Quaesitosaurus* (PIN 3906/2) are easily distinguished from *Vahiny* on the basis of characters of the occipital condyle, basal tubera, basisphenoid, and basiptyergoid processes (Fig. 6A, F). *Nemegtosaurus* exhibits a downward facing occipital condyle when the supraoccipital is oriented vertically, in contrast with the subparallel orientations of the skull roof and occipital condyle in *Vahiny*. The basal tubera in *Nemegtosaurus* and *Quaesitosaurus* are not separated by a bony sheet as they are in *Vahiny*, and the basiptyergoid processes are separated by a deep notch more similar to those of *Rapetosaurus* and *Malawisaurus* (SAM MAL 202). Finally, the openings for the internal carotid arteries are located between the basiptyergoid processes in *Nemegtosaurus*, rather than more laterally as in *Vahiny* (Wilson, 2005b).

Malawisaurus—*Malawisaurus* exhibits basiptyergoid processes that diverge via a deep notch and remain relatively straight throughout their length (SAM MAL 202; Gomani, 2005), as in *Rapetosaurus* and *Nemegtosaurus*. This contrasts with the broadened divergence of the basiptyergoid processes in *Vahiny*. *Vahiny* and *Malawisaurus* share the presence of a shallow posterior fossa between their basal tubera, but in *Malawisaurus* a midline ventral flange of bone overhangs the proximal end of the basiptyergoid process. This feature is absent in *Vahiny*.

Synopsis

Although *Vahiny* and *Rapetosaurus* coexisted in the same environment, both share their closest taxonomic affinities with titanosaurs that lived elsewhere. The cranial material of *Vahiny* indicates a close affinity to the Indian titanosaur *Jainosaurus* and South American titanosaurs *Muyelensaurus* and *Pitekunsaurus*. On the other hand, *Rapetosaurus* and *Isisaurus* share only general, more broadly distributed anatomical similarities with their respective contemporaries (*Vahiny* and *Jainosaurus*, respectively), or with each other. The hypothesized sister-taxon relationship between *Vahiny* and *Jainosaurus* requires testing in a phylogenetic context within a broad sample of titanosaurs. At

present, the anatomy supports the hypothesis that neither Madagascar nor India present evidence of an endemic fauna produced by long-term geographic isolation, as first noted by Depéret (1896a:485).

VAHINY AND MALAGASY 'TAXON B'

Initial evaluations of sauropod diversity in the Maevarano Formation recognized only one genus and species, '*Titanosaurus madagascariensis*,' on the basis of poorly preserved and dissociated postcranial elements (Boule, 1896; Depéret, 1896a, 1896b). As more remains were recovered in subsequent years, hints of at least one additional sauropod in the formation began to emerge. Thevenin (1907:pl. 1, fig. 16) figured a caudal vertebra that differed from one of those included in the '*T. madagascariensis*' syntype (UCB 92829) in its robustness, elongation, strong procoely, and straighter posterior neural arch margin. The figured centrum bore more similarities to UCB 92305, the smaller of the two centra described by Depéret (1896a:pl. 6, fig. 2). Based on the morphology of UCB 92305 and the vertebra figured by Thevenin (1907:pl. 1, fig. 16), Huene (1929) questioned the referral of the Malagasy sauropods to '*Titanosaurus*' and ultimately referred the materials in question to cf. *Laplataosaurus*, a sauropod he described from Upper Cretaceous of South America. This referral was based largely on the distinctiveness of the Malagasy titanosaur caudal vertebrae relative to those known from India and Patagonia referred to '*Titanosaurus*' (Huene, 1929:91).

Extensive excavations in the Maevarano Formation have yielded articulated and associated sauropod individuals as well as hundreds of isolated bones spanning hatchling to adult ontogenetic stages (Curry Rogers and Forster, 2001, 2004; Curry Rogers, 2005, 2009; Krause and Rasoamiamanana, 2006; Krause et al., 2006, 2010; Curry Rogers and Imker, 2007). Based on some of this new material, Curry Rogers and Forster (2001) described and named *Rapetosaurus krausei* on the basis of a well-preserved adult skull and a referred juvenile skull and its associated postcranial skeleton. Like Huene (1929), Curry Rogers and Forster (2001, 2004) recognized two caudal vertebral morphs in the syntypic material of '*Titanosaurus madagascariensis*,' and they tentatively referred one of the vertebrae (UCB 92829) to *Rapetosaurus*. Consistent with Huene's (1929) hypothesis, Curry Rogers and Forster (2001, 2004) speculated that the other caudal vertebral morph (UCB 92305) indicated a different titanosaur taxon that they informally referred to as 'Malagasy Taxon B' (Curry Rogers and Forster, 2001; Curry Rogers, 2002; Curry Rogers and Imker, 2007). Shortly after the naming of *Rapetosaurus*, Wilson and Upchurch (2003:146) posited that *Laplataosaurus madagascariensis* is a nomen dubium because it is not based upon associated, diagnostic material.

With regard to a second titanosaur taxon in the Maevarano Formation, several isolated vertebrae, girdle elements, and limbs that cannot be referred to *Rapetosaurus* have now been recovered (e.g., Curry Rogers, 2002; Curry Rogers and Imker, 2007). These enigmatic bones, which constitute less than 10% of the total sauropod collection from the unit, represent a variety of ontogenetic stages, and retain their distinctiveness from *Rapetosaurus* in both juvenile and adult form (Curry Rogers and Imker, 2007; McNulty et al., 2010). Despite their distinct morphology, we did not refer these isolated postcranial remains to *Vahiny depereti* in this report, and contend that assigning such disparate and dissociated elements to *Vahiny* at this time would likely propagate taxonomic problems. We restricted the holotype of *Vahiny* to the braincase, which can be directly compared and distinguished from the braincases of *Rapetosaurus* and other titanosaur. The name-bearing materials of *Vahiny depereti* are diagnostic and stable, which provides a testable hypothesis for future Malagasy titanosaur taxonomy. Field work in the Maevarano Formation is ongoing, and we anticipate that additional collection

of sauropod fossils will shed light on the relationship between the *Vahiny depereti* holotype and non-*Rapetosaurus* postcranial remains recovered from the Maevarano Formation.

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