First occurrence of stomach stones in pterosaurs

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FIRST OCCURRENCE OF STOMACH STONES IN PTEROSAURS

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ABSTRACT—Two nearly complete skeletons of the filter-feeding pterodactyloid *Pterodaustro guinazui* from the Lower Cretaceous of Argentina exhibit clusters of poorly sorted coarse sand to fine gravel inside the abdominal cavity. These stones are interpreted as ingested gastroliths (geogastroliths), which are commonly found in a variety of archosaurs (including birds) but have never before been reported in a pterosaur. The geogastroliths found in these *Pterodaustro* specimens are interpreted as having assisted in the digestion of hard food items such as 'shelled' crustaceans that are abundant in the fossil beds of this pterosaur. One of these specimens with geogastroliths has anterior mandibular teeth that are notably thicker than the posterior teeth and are somewhat procumbent. We suggest that these teeth might have facilitated the apprehension of fine gravel.

INTRODUCTION

Studies of gastroliths provide critical information for paleobiological inferences (Wings, 2004). These 'stomach stones' ('geogastroliths' of Wings, 2007) occur in terrestrial and aquatic animals, both extant and extinct, and have variously been interpreted as a source of mineral supply, ballast (in aquatic animals), for the maintenance of a microbial flora, for the elimination of parasites, hunger appeasement, and, most commonly, as grinding devices that assist in the digestion of hard food items. Living archosaurs (crocodiles and birds) frequently ingest fine gravel or very coarse sand. Gastroliths are not only widely distributed among living crocodiles (Taylor, 1993; Henderson, 2003) and birds (Gionfriddo and Best, 1999), but their presence has also been widely documented in a variety of extinct archosaurs, including ornithischians (Osborn, 1924; Cerda, 2008), prosauropods (Weems et al., 2007), sauropods (Wings and Sander, 2007), non-avian theropods (Ji et al., 1998; Kobayashi et al., 1999), and several lineages of extinct birds (Zheng et al., 2011).

Interestingly, gastroliths have not been reported for pterosaurs, a highly diverse group of Mesozoic archosaurs, whose evolutionary history spans more than 150 million years (Wellnhofer, 1991; Unwin, 2005). This study documents the first record of geogastroliths in a pterosaur, the filter-feeding ctenochasmatid *Pterodaustro guinazui*, known from hundreds of specimens from the Lower Cretaceous of central Argentina (Bonaparte, 1971; Chiappe et al., 2000). A newly collected specimen (MIC-V263) of this pterosaur shows a cluster of poorly sorted stones surrounded by ribs and gastralia that define the visceral cavity. Another specimen from an older collection (MIC-V243) reveals a few stones of varied size flanking disarticulated elements of the gastralia and ribs. In both specimens, the appearance and location of the stones support their interpretation as ingested gastroliths, thus providing the first evidence of this behavior among pterosaurs.

Institutional Abbreviations—MIC, Contacto: Museo Interactivo de Ciencias, Universidad Nacional de San Luis, San Luis, Argentina; **MMP**, Museo Municipal de Ciencias Naturales 'Galileo Scaglia,' Mar del Plata, Argentina; **PVL**, Instituto Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina.

SYSTEMATIC PALEONTOLOGY

PTEROSAURIA Kaup, 1834
PTERODACTYLOIDEA Plieninger, 1901
CTENOCHASMATIDAE Nopcsa, 1928
PTERODAUSTRO GUINAZUI Bonaparte, 1970
(Figs. 1–4)

Locality and Geological Setting—Both specimens (MIC-V263 and MIC-V243) come from exposures of the Lagarcito Formation along the Quebrada de Hualtarán, within the Sierra de las Quijadas National Park (northwestern San Luis Province, Argentina). MIC-V243 is from the 'Loma del *Pterodaustro*' fossil site (32°29′40.6″S, 66°59′38″W) and MIC-V263 is from a new site located 35 m from the 'Loma del *Pterodaustro*' (32°29′40.2″S). The fine-grained *Pterodaustro* beds of the Lagarcito Formation (medium siltstone to claystone, with very fine sand) are interpreted as having been formed within a shallow perennial lake developed in a flood plain under semiarid climatic conditions. The age of these deposits has been interpreted as Albian (Chiappe et al., 1998a, 1998b).

Available Material—Since the 1960s, nearly 300 specimens of the pterodactyloid *Pterodaustro guinazui* (cataloged in various Argentine institutions) have been collected from the Early Cretaceous 'Loma del *Pterodaustro*' fossil site and nearby localities in the San Luis Province of central Argentina (Bonaparte, 1971; Chiappe et al., 1998a, 1998b; Lopez-Arbarello and Codorniú, 2007). These specimens vary greatly in their degree of completeness, from rare, nearly complete and fully articulated skeletons to more common partial skeletons and abundant isolated elements; they also vary substantially in size and ontogenetic age. Six

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nearly complete and articulated specimens are known. These represent an almost complete growth series: from embryonic in ovo remains (i.e., MIC-V246; Chiappe et al., 2004; Codorniú et al., 2004) and juveniles with a wingspan shorter than 0.30 m (i.e., MIC-V241, MMP 1168; Codorniú and Chiappe, 2004) to subadult individuals (osteologically immature) of wingspans reaching 1.06 m (i.e., MMP 1089), 1.28 m (i.e., PVL 3860), and 1.59 m (i.e., MIC-V243). There are 67 partially complete, articulated specimens, including skulls, dorsal and sacral vertebral series, pectoral and pelvic girdles, and forelimbs and hind limbs. Most of the 215 specimens represented by isolated elements consist of bones from either extremities or individual vertebrae; the most common bones in the available sample are the humerus and metacarpal IV. Interestingly, proxies for full skeletal maturation are thus far present only in isolated elements (i.e., all complete or semicomplete specimens belong to osteologically immature individuals). These proxies include the complete fusion (lack of any sutural evidence) between the extensor tendon process and the shaft of the first wing phalanx, the complete fusion between the tibia and the proximal tarsals, and the fused distal secondary ossification centers of the humerus. Estimates of the wingspan of fully mature skeletons, based on regression models of complete and semicomplete specimens, indicate that *Pterodaustro guinazui* was able to reach a wingspan of at least 3 m—a value higher than previously estimated (e.g., Wellnhofer, 1991).

DESCRIPTION

The anatomy of MIC-V243 and MIC-V263 agrees in every respect with what has thus far been described for *Pterodaustro guinazui* (Bonaparte, 1971; Sánchez, 1973; Chiappe et al., 2000; Codorniú and Chiappe, 2004; Codorniú, 2005).

MIC-V263 comprises a partially complete and articulated skeleton in which the wingspan is estimated at 1.93 m (calculated by the sum of the main forelimb elements) (Fig. 1). This specimen preserves much of the rostrum, mandible and part of the mandibular dentition, a complete right wing and the distal portion of the left wing, the entire right hind limb and parts of its left counterpart (partial femur and tibia), portions of the right and left pelvic girdle (ilium, prepubis, and ischium), an articulated caudal series missing the most proximal portion, and a number of ribs, gastralia, and indeterminate bone fragments intermixed with geogastroliths (Figs. 1, 2). All the preserved major portions of this specimen are in articulation: the caudal vertebral series is aligned with the sacrum (mostly obscured by the mass of geogastroliths and surrounding bones; Fig. 2), the incomplete left hind limb is articulated to the pelvis and the complete right hind limb is fully articulated, the bones of both wings are articulated, and the bones of the anterior portion of the skull (premaxilla, maxilla, and dentary) are also in articulation. The specimen was found at the edge of a wash and there is no doubt that it would have been complete (see upper right corner of photograph in Fig. 1) if it were not because a portion of the slab was washed away prior to excavation.

MIC-V243 consists of an almost complete postcranial skeleton in which the wingspan is estimated at 1.59 m. In this specimen, both wings are almost complete and fully articulated (each extended in opposite directions from the torso) (Fig. 3). The axial skeleton and bones of the hind limbs are clustered, and only partially articulated, being positioned one on top another. The caudal vertebral series is articulated but detached from the sacrum and all the bones from the hind limb are articulated with one another. Next to the sternum, preserved in ventral view, is a cluster of ribs, gastralia, and geogastroliths (Fig. 3).

Based on the ontogenetic criteria of Bennett (1993) that are preserved in MIC-V263 and MIC-V243, both specimens are interpreted as osteologically immature individuals. In MIC-V263, the extensor tendon process and the shaft of the first wing phalanx are clearly individualized—in fact, it seems as if the extensor

TABLE 1. Measurements (in mm) of maximum lengths of right skeletal elements of MIC-V263 and MIC-V243.

Elements	MIC-V263	MIC-V243	Elements	MIC-V263	MIC-V243
Skull			Hind limb		
dn	316.0^P	—	Fe	94.0	78.8
mx	300.0^P	—	ti	145.0	129.5
Forelimb			mtI	73.7	—
hu	112.0	86.5	mtII	72.0	—
ul	154.0	129.0	mtIII	70.6	—
ra	152.0	129.0	mtIV	65.5	—
pt	99.0^P	84.5^P	mtV	17.0	13.5
mcI	114.5	95.0	ph1d1	16.5	—
mcII	97.5^P	95.0	uphd1	6.5	8.2
mcIII	97.5^P	—	ph1d2	16.3	—
mcIV	117.0	100.6	ph2d2	12.5	—
wph1	182.0	152.3	uphd2	7.7	8.3
wph2	175.0	143.5	ph1d3	18.5	—
wph3	132.0	112.1	ph2d3	4.5	4.6
wph4	93.0	88.8	ph3d3	11.0	10.0
ph1d1	17.3	13.3	uphd3	7.3	8.5
uphd1	6.7	9.0	ph1d4	21.0	—
ph1d2	16.0	14.0	ph2d4	4.5	—
ph2d2	10.0	10.0	ph3d4	4.0	4.0
uphd2	6.0	7.0	ph4d4	10.5	10.0
ph1d3	17.5^e	—	uphd4	7.2	8.7
ph2d3	—	5.5	uphd5	7.4	—
ph3d3	—	8.4			
uphd3	7.0	7.0			

Abbreviations: **dn**, dentary; **fe**, femur; **hu**, humerus; **mcI–IV**, metacarpals I–IV; **mtI–V**, metatarsals I–V; **mx**, maxilla; **phd**, non-ungual phalanx of manual and pedal digits (e.g., ph1d1 means phalanx 1 of digit 1); **pt**, pteroid; **ra**, radius; **ti**, tibia; **ul**, ulna; **uphd**, ungual phalanx of manual and pedal digits; **wph1–4**, wing phalanx 1–4 of wing finger (manual digit IV). Wingspans: MIC-V263 = 193 cm and MIC-V243 = 160 cm. (**e**, estimated length; **p**, preserved length).

tendon process was not even partially coossified to the shaft of this bone. The tibia and proximal tarsals of this specimen are also not fused to one another. In the smaller MIC-V243, the pelvic girdle is not fused to the sacrum even though the ischiopubic plate is fused to the ilium. The coracoid and scapula of this specimen are not fused to one another and neither are the tibia and the proximal tarsals. These skeletal conditions suggest that neither specimen had reached skeletal maturity at the time of death, despite having wingspans of nearly 2 m (MIC-V263) and 1.6 m (MIC-V243) (for measurements, see Table 1).

MIC-V263 contains 29 variably sized (long axis ranges from 1.5 to 8.4 mm, >86% of them range between 1.5 and 6.0 mm; Table 2) and variously colored pieces of fine gravel, clustered within an area of approximately 24 cm^2. These stones, for the most part embedded in light greenish gray mudstone, are surrounded by gastralia and some thoracic ribs, and are located just in front of the pelvic elements and above the prepubis (Fig. 2). Sedimentary color differences between the moderate orange-pink (10R 7/4, Munsell color system) and light brown (5YE 6/4) of the slab and the light greenish gray (5GY 8/1) containing the geogastrolith aggregate are explained as the result of post-sedimentary chemistry (reduction stain). A smaller cluster of relatively fine gravel is also preserved on top of the ischium of this specimen (Table 2). Most stones are composed of lightly colored quartz (only one corresponds to feldspar) and all show a small degree of abrasion, although most of them present distinctly angular edges. A few stones are preserved in proximity to the disarticulated elements distributed in the visceral cavity of MIC-V243. Most stones are encased within a gray-green mudstone and differ in size, color, and degree of abrasion. These stones fall within the size range of those preserved within MIC-V263 and have the same basic characteristics.
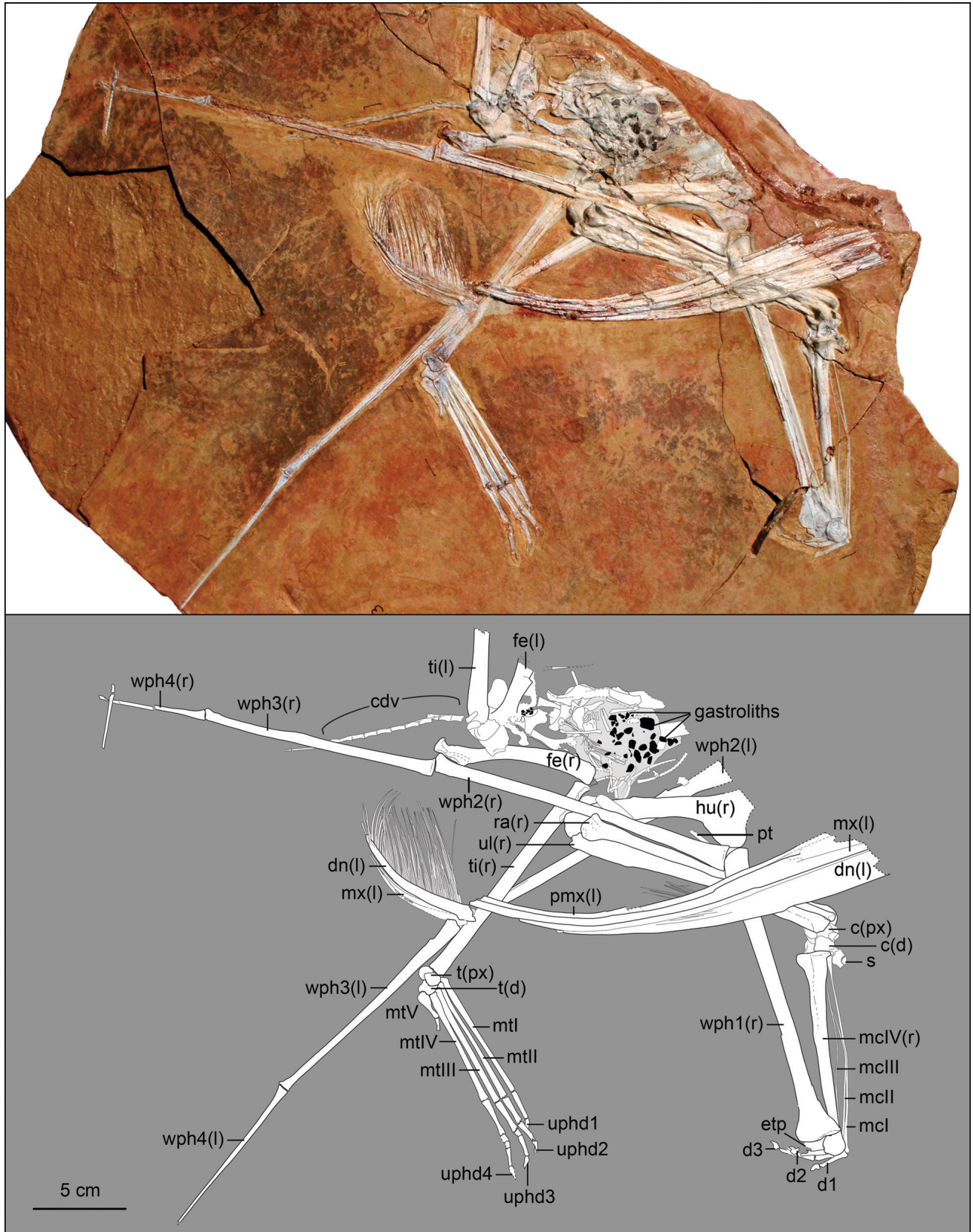
FIGURE 1. Photograph and interpretive drawing of *Pterodaustro guinazui*, MIC-V263. The preserved geogastroliths are denoted in black. Note the reduction stain highlighted in light gray in the interpretive drawing. **Abbreviations**: **c(d)**, distal carpals; **cdv**, caudal vertebrae; **c(px)**, proximal carpals; **d1–3**, digits 1–3; **dn**, dentary; **etp**, extensor tendon process; **fe**, femur; **hu**, humerus; **mcI–IV**, metacarpals I–IV; **mtI–V**, metatarsals I–V; **mx**, maxilla; **pmx**, premaxilla; **ra**, radius; **s**, sesamoid; **t(d)**, distal tarsals; **ti**, tibia; **t(px)**, proximal tarsals; **ul**, ulna; **uphd1–4**, ungual phalanx of digits 1–4; **wph1-4**, phalanges 1–4 of wingfinger. **(r)** or **(l)** refer to the right or left side, respectively. (Color figure available online.)

FIGURE 2. Photograph and interpretive drawing of the geogastroliths (denoted in black) contained within the gastrointestinal tract of MIC-V263. The number assigned to each stone corresponds to that shown in Table 2 (geogastroliths preserved in association with the ischium are preceded by the letter 'i'). Geogastroliths 1 and 6 were subsequently removed for SEM imaging. Note the reduction stain highlighted in light gray in the interpretive drawing. **Abbreviations**: **ac**, acetabulum; **fe**, femur; **ga**, gastralia; **il**, ilium; **isc**, ischium; **pap**, postacetabular process; **pre**; prepubis; **ri**, ribs; **sv**, sacral vertebrae. (Color figure available online.)
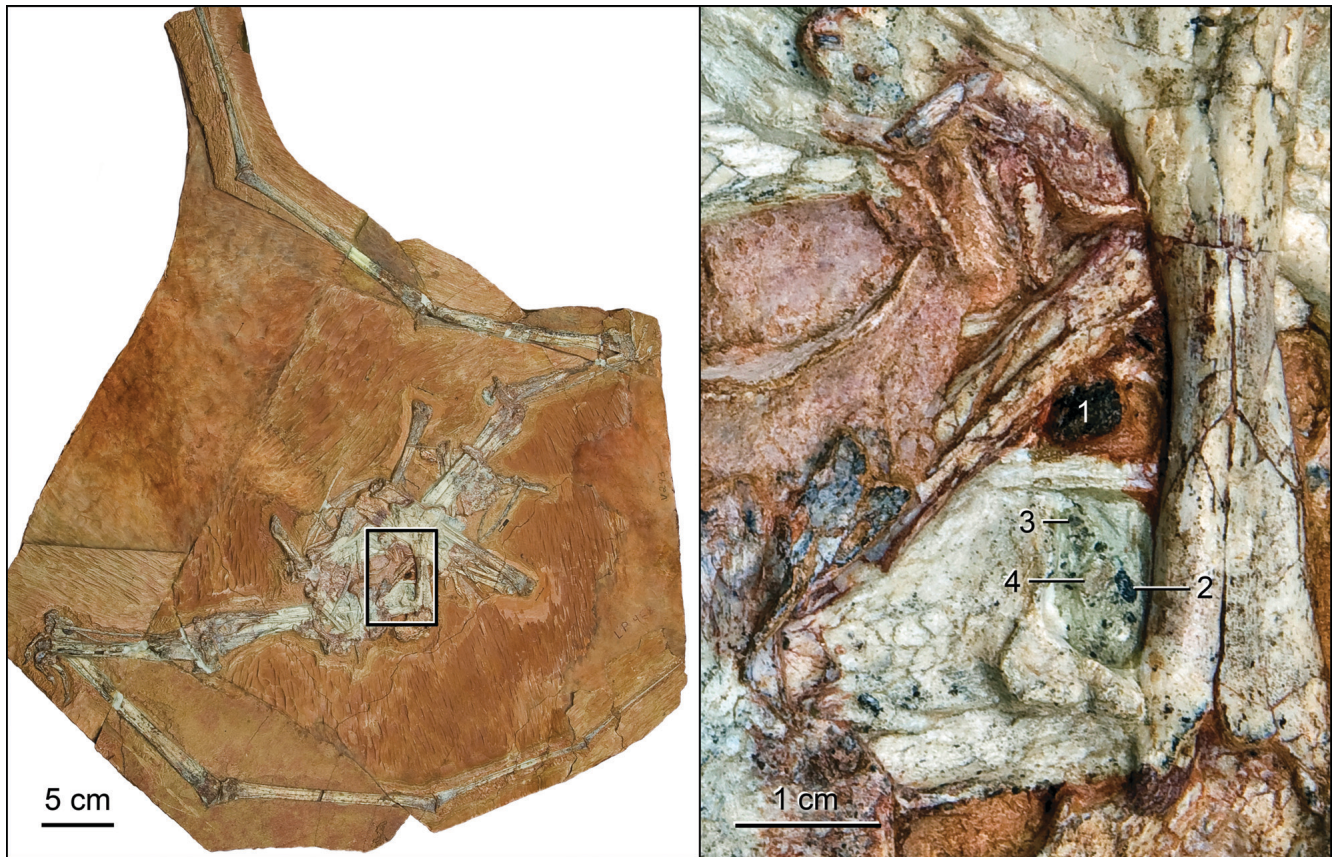
FIGURE 3. Complete slab and detail of the region containing geogastroliths (inset) of MIC-V243. The number assigned to each stone corresponds to that shown in Table 2. Note the reduction stain at the center of the photograph. (Color figure available online.)

DISCUSSION

Several criteria support the interpretation of the fine gravel found in MIC-V263 as geogastroliths. First, these stones are located within the abdominal cavity of an almost complete and partially articulated skeleton (Category 1 of Wings, 2004). Second, the reduction stain that characterizes the matrix surrounding these stones suggests that they were contained in a single structure (presumably part of the gastrointestinal tract). Third, fossils from the *Pterodaustro* beds of the Lagarcito Formation are found in fine-grained reddish claystone of lacustrine origin, in which transported pebbles are extremely rare. Furthermore, the interpretation of such fine gravel as geogastroliths is also supported by the association of stones of similar appearance with bones defining the abdominal cavity of MIC-V243 (Fig. 3).

A wide range of functions has been attributed to gastroliths. However, assistance in digestion and processing of food, mainly crushing and grinding, is the most frequently proposed function for geogastroliths among fossil vertebrates (Wings, 2007). This functional interpretation has widespread consensus among ornithologists (Gionfriddo and Best, 1999). Many living birds (granivorous, herbivorous, carnivorous, and/or insectivorous) are known to ingest grit or variably sized stones (Norris et al., 1975; Torre et al., 1991; Best, 1995; Gionfriddo and Best, 1999; Best and Stafford, 2002; Gurd, 2006; Wings, 2007; Beaune et al., 2009). This behavior has been well documented in filter-feeding birds such as flamingos (Jenkin, 1957; Suárez and Urios, 1999), which on the basis of (i) phylogeny (birds are the closest living relatives of pterosaurs), (ii) diet (filter-feeding specializations), and (iii) size (wingspans of flamingoes fall within the known range

for specimens of *Pterodaustro*), are considered to be suitable modern analogues for *Pterodaustro* (Wellnhofer, 1991; Unwin, 2005). It is thus noteworthy that among specimens of the Greater Flamingo (Phoenicopteridae), the number and size of the gastroliths are similar to those found in *Pterodaustro*. For instance, Jenkin (1957) reported that at least 80% of the gastroliths found in Greater Flamingoes from Kenya ranged between 0.5 and 4 mm and only a few of them exceeded 5 mm. Additionally, Suárez and Urios (1999) found a comparable size range (0.5–6 mm) in the gastroliths of another population of Greater Flamingos from Spain. The presence of a cluster of smaller stones preserved in the pelvic region of MIC-V263 suggests that, as in birds (Norris et al., 1975; Best, 1995; Best and Stafford, 2002), these stones passed through the gastrointestinal tracts of *Pterodaustro*; this has also been documented for other reptiles (Fitch-Snyder and Lance, 1993; Valido and Nogales, 2003). In birds, grit consumption and excretion is influenced by both diet (Norris et al., 1975; Skead and Mitchell, 1983; Alonso, 1985; Norman and Brown, 1985; Hogstad, 1988; Gionfriddo and Best, 1995, 1996; VerCauteren et al., 2003) and environmental conditions (Best and Gionfriddo, 1994; Best et al., 1996). These data are not available for flamingos, but grit retention in other species is typically short; most grits are rapidly replaced, usually within five days of ingestion (Gionfriddo and Best, 1995). Therefore, it is likely that the stones found in the pelvic region of MIC-V263 were located within the distal portion of the gastrointestinal tract and soon to be excreted. The pattern of grit excretion (the size of stones that are retained or expelled from the gastrointestinal tract) is variable among living birds, but many birds excrete primarily the smallest stones (Best

FIGURE 4.   Detail of the anterior portion of the mandible and dentition of MIC-V263. Numbers indicate the first through sixth dentary teeth; (r) and (l) refer to the right or left side, respectively. Those teeth of which the side is not indicated belong to the left dentary. (Color figure available online.)

and Gionfriddo, 1991). We suggest, therefore, that, as in birds, the geogastroliths of *Pterodaustro* were probably replaced on a regular basis, and that the smallest stones would have been the most frequently excreted.

How *Pterodaustro*, with its highly specialized dentition (Bonaparte, 1971; Chiappe et al., 2000), ingested the geogastroliths is uncertain. However, the unusual morphology of the anterior-most portion of the mandible of MIC-V263 and the dentition that it bears allows us to propose a possible solution to this problem. The first seven teeth of this specimen have a distinctly different morphology from the filament-like teeth that characterize the main part of the dentition in the mandible of this pterosaur (Chiappe et al., 2000). The anterior-most teeth are thicker and they are set in individual alveoli. Whereas the first two teeth are nearly straight and anteriorly directed, the following five teeth are longer and strongly curved backwards, collectively forming a procumbent, shovel-like structure (Fig. 4). We hypothesize that this morphology helped the animal to acquire the stones it ingested.

Whereas direct evidence of diet is not available for any specimen of *Pterodaustro*, the unique structure of its jaws (a sieving basket made up of hundreds of long, filament-like teeth set in up-curved dentaries) has consistently been interpreted as a sophisticated filter-feeding specialization (Sánchez, 1973; Wellnhofer,

1991; Chiappe et al., 2000; Unwin, 2005). Given the abundance of clam and seed shrimp in the Lagarcito Formation, Chiappe et al. (1998b) speculated that these minute 'shelled' crustaceans formed part of the diet of *Pterodaustro*. Considering the possible functions that have been reported for geogastroliths in vertebrates (Wings, 2007), and that these crustaceans have hard chitinous or calcareous valves, it is reasonable to assume food processing as a probable function of the geogastroliths found in *Pterodaustro*.

It is unclear whether or not the apparent absence of geogastroliths in other pterosaurs is the result of taphonomic bias. Dental and phylogenetic considerations suggest that ingestion of sand and gravel may have also been part of the behavioral repertoire of other ctenochasmatids; however, to date these pterosaurs have been largely represented by incomplete specimens, primarily known from cranial remains (e.g., *Gegepterus changae* [Wang et al., 2007], *Beipiaopterus chenianus* [Lü, 2003], *Elanodactylus prolatus* [Andres and Ji, 2008], *Gladocephaloides jinganshanenesis* [Lü et al., 2012], and several European ctenochasmatids [Wellnhofer, 1970; Bennett, 2007]). Nonetheless, considering that hundreds of exceptionally well-preserved examples of pterosaurs lacking gastroliths have been found worldwide (Wellnhofer, 1991; Unwin, 2005), it is reasonable to conclude that such behavior was probably rare among pterosaurs.

TABLE 2.   Measurements (in mm) of the geo-gastroliths of MIC-V263 and MIC-V243.

Specimen	Region	Geo-gastrolith number	Longest axis	Shortest axis	Composition
V263	Gastralia and thoracic ribs	1	7.4	7.2	Feldspar
		2	4.5	2.5	Metaquartzite
		3	4.6	3.0	Metaquartzite
		4	5.0	4.0	Metaquartzite
		5	3.5	2.0	Metaquartzite
		6	5.5	4.0	Metaquartzite
		7	5.0	4.0	Metaquartzite
		8	8.4	4.0	Metaquartzite
		9	5.0	5.0	Metaquartzite
		10	5.0	1.5	Metaquartzite
		11	2.5	2.0	Metaquartzite
		12	5.5	3.5	Metaquartzite
		13	8.2	4.5	Metaquartzite
		14	5.5	3.0	Metaquartzite
		15	5.4	3.0	Metaquartzite
		16	4.0	2.5	Metaquartzite
		17	1.5	0.5	Metaquartzite
		18	2.0	1.5	Metaquartzite
		19	6.0	3.5	Metaquartzite
		20	7.0	4.0	Quartz
		21	4.5	3.0	Metaquartzite
		22	4.0	3.0	Quartz
		23	4.0	3.0	Metaquartzite
		24	2.0	1.0	Metaquartzite
		25	6.0	3.0	Feldspar?
		26	4.5	2.0	Quartz
		27	3.3	2.6	Feldspar?
		28	4.0	2.5	Metaquartzite
	Ischium (i)	29	4.5	2.5	Metaquartzite
		i1	2.0	1.6	Metaquartzite
		i2	2.7	1.5	Metaquartzite
		i3	2.8	1.4	Metaquartzite
		i4	2.0	0.8	Quartz
		i5	1.6	1.5	Metaquartzite
		i6	1.1	0.8	Metaquartzite
		i7	0.7	0.5	Metaquartzite
V243		1	6.5	5.0	Schist
		2	2.0	1.0	Metaquartzite
		3	1.5	1.0	Schist
		4	3.5	2.0	Metaquartzite

Geo-gastrolith numbers corresponds with those figured in Figures 2 and 3.

CONCLUSION

The present study documents the first evidence indicating that, like birds and many other archosaurs, some pterosaurs swallowed stones that were retained in the gastrointestinal tract for a period of time. The procumbent shape of the most anterior mandibular teeth of MIC-V263 and the relatively narrow size range of the preserved geogastroliths suggests that selected fine gravel could have been captured by the action of the animal's lower jaw. The presence of geogastroliths in two specimens of *Pterodaustro*, and their inferred role in assisting digestion, is consistent with the interpretation of this pterosaur as a filter-feeder, with a diet that may have included hard items such as 'shelled' crustaceans. This discovery once again highlights the remarkable ecomorphological specializations that have evolved in some members of the Pterosauria.

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