CONTRIBUTIONS IN SCIENCE

CRANIAL MORPHOLOGY OF PTERODAUSTRO GUINAZUI (PTEROSAURIA: PTERODACTYLOIDEA) FROM THE LOWER CRETACEOUS OF ARGENTINA

Luis M. Chiappe, Alexander W. A. Kellner, David Rivarola, Sergio Davila, and Marilyn Fox
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CRANIAL MORPHOLOGY OF *PTERODAUSTRO GUINAZUI* (PTEROSAURIA: PTERODACTYLOIDEA) FROM THE LOWER CRETACEOUS OF ARGENTINA

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ABSTRACT. With hundreds of filament-like teeth in its mandibles and several other unique cranial features, the Argentine Early Cretaceous *Pterodactylus guinazui* ranks among the most specialized of pterosaurs. Based on newly collected specimens, this study provides a detailed description of the peculiar skull morphology of *Pterodactylus* and discusses its phylogenetic position within pterosaurs. An overview of the stratigraphy, sedimentology, and chronology of the Lagarocito Formation from which *Pterodactylus* comes is provided, along with an interpretation of the paleoenvironment. Cranial morphology corroborates the sister-taxon relationship between *Pterodactylus* and the Late Jurassic *Ctenochasma* proposed by most previous authors.

RESUMEN. Con cientos de dientes filamentosos en sus mandíbulas y varios otros caracteres cranean-distintivos, *Pterodactylus guinazui* del Cretácico temprano de Argentina, es uno de los pterosaurios más especializados. Sobre la base de ejemplares recientemente colectados, este estudio provee una descripción detallada de la peculiar morfología craneana de *Pterodactylus* y analiza sus relaciones filogenéticas dentro de los pterosaurios. También se provee una reseña estratigráfica, sedimentológica, y cronológica de la Formación Lagarocito—la formación portadora de *Pterodactylus*—junto con una interpretación del paleoambiente. La morfología craneana corrobora la relación de grupo hermano entre *Pterodactylus* y *Ctenochasma*, del Jurásico tardío, que fuera propuesta por la mayoría de los autores previos.

INTRODUCTION

Paleontological expeditions led by J.F. Bonaparte in the late 1960s and early 1970s made a significant contribution to the knowledge of pterosaur evolution with the discovery of the spectacular pterodactyloid *Pterodactylus guinazui* Bonaparte, 1970 (original spelling emended by Wellnhofer [1978] following the guidelines of the ICZN). Collected from the banks of a creek cutting through beds of the Lagarocito Formation at a site known today as Loma del *Pterodactylus*, in what is now the Parque Nacional Sierra de las Quijadas (Fig. 1), *Pterodactylus* was the first pterosaur to be found in Argentina. When discovered, *Pterodactylus* represented only the second record of pterosaurs from South America (Price, 1971). Most importantly, *Pterodactylus* provided strong evidence that pterosaurs had evolved a filter-feeding morphology uncommon among tetrapods.

Twenty-five years after Bonaparte’s exploratory expeditions to the Mesozoic deposits of the central Argentine province of San Luis, three large-scale excavations (in 1994, 1996, and 1998; see Chiappe et al., 1998a, b) were conducted at the quarry in the Loma del *Pterodactylus* where the first specimens of *Pterodactylus* were collected (Fig. 1). These excavations produced hundreds of skeletal remains of this pterosaur, including adult, juvenile, and neonate specimens (Chiappe et al., 1998b).

Despite the availability of material of *Pterodactylus* (even before the newly collected specimens) and the fact that this multitoothed pterosaur has consistently been used as a startling example of morphological specialization within this group (e.g., Benton, 1990; Wellnhofer, 1991; Chiappe and Chinsamy, 1996), the cranial anatomy of *Pterodactylus* has received little attention beyond early descriptions by Bonaparte (1971) and Sanchez (1973). The recent expeditions to Loma del *Ptero-*
daustro collected several skulls and jaws of adult individuals. These are described here in detail. We also review previous anatomical data on this taxon in light of these specimens and discuss the phylogenetic position of *Pterodaustro* among pterodactyloids.

Institutions are abbreviated as follows: PVL, Sección Paleontología de Vertebrados, Instituto Miguel Lillo (San Miguel de Tucumán, Argentina); and MHIN-UNSL-GEO, Museo de Historia Natural, Universidad Nacional de San Luis (San Luis, Argentina).

GEOLOGICAL SETTING OF THE LAGARCITO FORMATION

The Lower Cretaceous rocks of the Argentine Province of San Luis form a geotectonic unit known as the San Luis Basin (Flores and Criado Roque, 1972). This basin has been interpreted as a rift basin resulting from cortical stresses generated during

Figure 1 Geographic distribution of the Lagarcito Formation and location of the Loma del *Pterodaustro* fossil site

the breakup of Gondwana (Ramos, 1990). Lithologically, this basin corresponds to a typical continental sequence of red beds exceeding 1,000 meters in thickness. These rocks crop out in several ranges grouped under the name Cordon de Serranias Occidentales, which extend in a north–south direction over roughly 300 kilometers (Fig. 1).

Stratigraphically, the Lower Cretaceous rocks of San Luis are divided into the Gigante Group and the Lagarcito Formation (Flores and Criado Roque, 1972; Fig. 2), which comprise the entire duration of two cycles of infilling of a continental basin (Rivarola, 1994). These cycles represent two depositional megasequences involving environments that range from alluvial fans associated with alluvial plains to fluvial plains and lacustrine environments. Rocks of the Gigante Group form most of the two megasequences, and they are composed of conglomerates, sandstones, claystones, and evaporites. The Lagarcito Formation forms the top section of
the second megasequence, and it is formed by fine sediments developed under fluvo-lacustrine environments associated with limited development of aeolian dunes.

In the Sierra de Las Quijadas, the Lagarcito Formation is best exposed at Quebrada de Hualtarán (Fig. 1). In this area, 45 meters of continuous sediments of sandstones and mudstones, representing at least three fluvo-lacustrine sequences, rest over a basaltic flow dated between 107.4 and 109.4 Ma (Yrigoyen, 1975).

Most fossils from the Lagarcito Formation have been excavated at a small site (~50 m²). This site has become known as Loma del Pterodaustro (Chiappe et al., 1995). The Loma del Pterodaustro fossil site corresponds to the basal 8 meters of the section of the Lagarcito Formation at Quebrada de Hualtarán (Fig. 2). A detailed sedimentological study of these deposits has been presented elsewhere (Chiappe et al., 1998a). Three lithofacies can be recognized from base to top: Facies 1, inversely graded, massive sandstones to massive, matrix-supported conglomerates with lenticular geometry and disordered fabric; Facies 2, fine-grained sandstone with a flat top and base, and asymmetric ripples; and Facies 3, massive to laminated claystones, siltstones, and very fine sandstones, which represent a thickening and coarsening upward sequence. Facies 1–3 have been interpreted as debris flows, sheetfloods deposited in a sand-flat near the shore, and a typical lake sequence, respectively. With very few exceptions, all fossils from Quebrada de Hualtarán come from Facies 3 (Chiappe et al., 1998a, b). This facies has been subdivided into three subfacies of low-energy deposits (Fig. 2). One of them (F3.1; Fig. 2) is composed of laminated, very fine sediments entombing the majority of fossils. This subfacies was interpreted as forming in the offshore portion of a lake.

BIOTA, PALEOENVIRONMENT, AND CHRONOLOGY OF THE LAGARCITO FORMATION AT LOMA DEL PTERODAUSTRO

The fine sandstones and claystones of the Lagarcito Formation at Loma del Pterodaustro have provided abundant fossil remains (Chiappe et al., 1995, 1998a, b). These include a diverse array of trace fossils, plant remains, conchostracans, ostracods, and various vertebrates. Among the vertebrate fauna are semionotid and pleuropholid fishes, anurans,
and abundant pterosaur remains, most of which are probably of *Pterodaustro*. Preservation of delicate structures such as the needlelike mandibular teeth of *Pterodaustro* and the imprints of stems and reproductive plant structures led to the classification of these beds as a *Konservat Lagerstätte sensu* Seilacher et al. (1985) (see also Seilacher, 1990; Chiappe et al., 1995, 1998a).

The facies association of the lower section of the Lagarkito Formation, along with the absence of evidence of subaerial exposure and evaporite layers, suggest that rocks at Loma del *Pterodaustro* correspond to a fluvo-lacustrine sequence of long duration. Preservation of laminations in subfacies 3.1 indicates that the lake was at least periodically thermally stratified, and it may have developed an anoxic bottom that prevented destruction of the laminations and favored preservation of delicate structures.

The lower section of the Lagarkito Formation, at Quebrada de Hualtarán, is interpreted as a complete sequence of transgression and expansion of a perennial lake over an alluvial sandy flat, followed by its gradual infilling and shallowing during a highstand period of the lacustrine system. The predominant climate during deposition of the Lagarkito Formation is interpreted as semiarid and seasonal (Chiappe et al., 1998a).

Originally, the Lagarkito Formation was placed in the Tertiary (Flores, 1969). After the discovery of *Pterodaustro guinauzi*, Bonaparte (1970) placed this unit within the Upper Jurassic on the basis of similarities between this pterosaur and Late Jurassic pterodactyloids. Subsequently, with the discovery of an Aptian–Albian palynoflora in the underlying La Cantera Formation (Gigante Group) and the Early Cretaceous dates for the basalt at Quebrada de Hualtarán, Yrigoyen (1975) placed the Lagarkito Formation within the Upper Cretaceous, and Bonaparte (1978) allocated those strata to the Lower Cretaceous. Recent interpretations, combining sedimentological, stratigraphical, and paleontological data, have adjusted the chronology of this lithostratigraphic unit, supporting an Albian age (see Chiappe et al. [1998a] for a more extensive discussion of the age of these beds).

**CRANIAL ANATOMY OF PTERODAUSTRO GUINAUZI**

This study is mostly based on recently collected material, including a skull and jaw (MHN-UNSL-GEO-V-57), another skull and jaw missing their rostral halves (MHN-UNSL-GEO-V-135), and an isolated, nearly complete jaw (MHN-UNSL-GEO-V-175). As in other known skulls of *Pterodaustro*, the new crania and jaws are flattened, preserved essentially in two dimensions. Many of the bones are broken, thus complicating identification between sutures. In MHN-UNSL-GEO-V-57 and MHN-UNSL-GEO-V-135 the skull is exposed on its left side; only a few right bones are visible. In MHN-UNSL-GEO-V-57 the left mandible is exposed laterally, whereas in MHN-UNSL-GEO-V-135 the right one is exposed. MHN-UNSL-GEO-V-175 exposes its left side.

**SKULL**

The skull of *Pterodaustro* is characterized by a remarkably long, slender, and upwardly curved preorbital region, which comprises more than 85 percent of the skull length (Figs. 3, 4). MHN-UNSL-GEO-V-57 (Fig. 3) has a total cranial length of almost 29 cm. This is approximately 20 percent larger than that of PVL-3860, the most commonly figured specimen of *Pterodaustro* (Sanchez, 1973; Bonaparte, 1978; Wellnhofer, 1991). MHN-UNSL-GEO-V-135 (Fig. 5) is somewhat (~10 percent) larger than MHN-UNSL-GEO-V-57. The nasoantorbital fenestra in this taxon is comparatively small (Kellner, 1993), reaching between 10 and 12 percent of the total skull length. Because the skull is flattened, no detailed information regarding the temporal openings is available.

In lateral view, the snout curves gently upward (Figs. 3–5). A long premaxilla and maxilla, whose suture is not discernible in any of the available specimens, form the snout. As in other pterosaurs (Wellnhofer, 1978), the slender premaxilla forms the entire dorsal margin of the snout, approaching the rostral margin of the orbit. In MHN-UNSL-GEO-V-57 it is uncertain whether the premaxilla was toothed or not because the most rostral end of the snout is not preserved. Unfortunately, none of the remaining known skulls clarify this issue. In MHN-UNSL-GEO-V-57 both premaxillae seem to be fused to each other for most of their length. Sanchez (1973) reported a thin, caudal tongue of the maxilla contacting the nasal and excluding the premaxilla from the nasoantorbital fenestra (Figs. 6A, 7). This condition, which is different from that of most pterosaurs (e.g., Wellnhofer, 1978; Wellnhofer and Kellner, 1991), has not been corroborated by either of the new specimens, in which the premaxilla forms the dorsal margin of the nasoantorbital fenestra (Figs. 6B, 8, 9). Also differing from previous interpretations (Sanchez, 1973), the premaxilla is extended farther caudally over the rostral half of the orbit (cf. Figs. 6A, B, 8).

The maxilla forms most of the lateral surface of the snout (Figs. 3–5, 7). This bone tapers rostrally from the rostral margin of the nasoantorbital fenestra. In all available specimens the suture between this bone and the rostral end of the jugal is not clear. In fact, these two bones appear to be

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*Figure 3* Skull and jaws of *Pterodaustro guinauzi* (MHN-UNSL-GEO-V-57) in left lateral view. Scale bar = 5 centimeters
Figure 4 Camera lucida drawing of the skull and jaws of *Pterodaustro guinazui* (MHIN-UNSL-GEO-V-57) in left lateral view. Abbreviations: A, angular; AR, articular; D, dentary; F, frontal; J, jugal; L, lacrimal; MX, maxilla; N, nasal; NOF, nasoantorbital fenestra; P, parietal; PMX, premaxilla; PO, postorbital; POF, postfrontal; POP, paraoccipital process; Q, quadrate; SO, supraorbital; SQ, squamosal; SR, sclerotic ring.
fused to each other. However, a thin tongue of the maxilla projects caudally beneath the jugal, reaching the caudal margin of the nasoantorbital fenestra (Figs. 6B, 8). The maxilla bears hundreds of tiny teeth, which in MHIN-UNSL-GEO-V-57 extend from the rostral end of the maxilla to near the rostral margin of the nasoantorbital fenestra (Fig. 4). Thus, the caudal extension of the maxillary tooth row of this specimen extends much more than that illustrated by Sanchez (1973) in her skull reconstruction (Fig. 7).

The dorsocaudal corner of the nasoantorbital fenestra is formed by a subtriangular nasal (Figs. 6-9). This element has a comparatively long, thin rostral process that reaches the center of the nasoantorbital fenestra, underlying the premaxilla (Figs. 6B, 9). Ventrally, the nasal tapers into a thin process that fails to reach the jugal, although it ends very close to it (Sanchez, 1973). The contact of the right nasal and jugal in MHIN-UNSL-GEO-V-57 (Fig. 6B) is not natural and can be regarded as a result of deformation during crushing. The morphology of the ventral nasal process is similar to that of archaeopterodactyloids (sensu Kellner, 1996, 1997) such as Pterodactylus Cuvier, 1809, and Germanodactylus Young, 1964. All more derived pterodactyloids, which are members of the Dsungaripteroidea (Young, 1964; Kellner, 1996), have either displaced this nasal process medially (e.g., Anhanguera Campos and Kellner, 1985) or have almost lost it (e.g., Quetzalcoatlus Lawson, 1975) (see Kellner and Langston, 1996).

The lacrimal of Pterodaustro is wedged between the nasal, prefrontal, and jugal. This bone has three distinct processes: a short rostral one, a longer and wider caudal one, and a hook-shaped ventral one (Figs. 6B, 8, 9). Although now flattened, in life the ventral process probably extended slightly lateral to
the orbit, as seen in some other pterosaurs known from less distorted specimens (e.g., Anhanguera). In MHIN-UNSL-GEO-V-57 (Fig. 6B), this process is significantly more robust than the process illustrated by Sanchez (1973; Fig. 6A), which agrees more with that of MHIN-UNSL-GEO-V-135 (Fig. 9). MHIN-UNSL-GEO-V-135 clearly shows that the bone identified as a prefrontal by Sanchez (1973) is, in fact, the dorsal exposure of the caudal process of the lacrimal (Fig. 9).

Rostrally, both frontals are united by a suture that becomes indistinguishable in the caudal half. Caudally, the frontals are wedged between the postfrontals and parietals (Figs. 6, 8).

The parietals in both specimens are very crushed, making their edges difficult to interpret, particular-
ly in their caudal region. As far as they can be observed, both elements are fused to each other along the midline. Although the boundaries of this bone were not clearly illustrated by Sanchez (1973; Fig. 7), the new specimens indicate that the parietal forms the medial margin of the supratemporal fenestra (Fig. 6B), as in most archosaurs (Romer, 1956). Interestingly, the caudal region of the parietals of all available specimens, including those previously described by Bonaparte (1971) and Sanchez (1973), is slightly extended as a thin bony lamina (Figs. 6, 8, 9). Although some of this appearance results from crushing, it cannot be ruled out that the parietals projected caudally as a small crest. Even if this interpretation is correct, this parietal crest would have been very small and not as developed as in some other pterosaurs (e.g., Gallopliopterus Fabre, 1974).

Caudal to the lacrimal, there is a flattened bone, here interpreted as the prefrontal. Based on MHIN-UNSL-GEO-V-57, this bone would correspond to the rostral portion of what Sanchez (1973) interpreted as the supraorbital (Fig. 6A). The slender supraorbital does indeed line the dorsal margin of the orbit and precludes the frontal from the orbital margin (Sanchez, 1973), but it does not appear to extend rostrally to reach the lacrimal (Fig. 6B).

In MHIN-UNSL-GEO-V-57, the postfrontal is a suboval element that contacts the frontal medially and the parietal caudally and is partially overlain by the postorbital (Fig. 6B). A caudally oriented process of the postfrontal, as illustrated by Sanchez (1973), was not observed in the new specimens.

The postorbital is a triradiate element (Fig. 6B). Its dorsal process is slightly expanded and abuts against the parieto-postfrontal suture. The ventral process overlies the dorsocaudal process of the jugal, whereas the caudal process overlies the lateral surface of the squamosal. The unusual condition of having the postorbital completely separated from the frontal by the postfrontal (Figs. 6B, 8), also indicated by Sanchez (1973; Fig. 6A), distinguishes Pterodaustro from other pterosaurs (Wellnhofer, 1978; Wellnhofer and Kellner, 1991).

The jugal is a conspicuous bone that forms the ventrocaudal and ventral margins of the nasoantorbital fenestra and the orbit, respectively, and the rostroventral corner of the infratemporal fenestra (Fig. 6A). The jugal has four distinct processes (Figs. 8, 9). The rostral process forms the ventral margin of the nasalantorbital fenestra and, in MHIN-UNSL-GEO-V-135, projects rostrally beyond the nasoantorbital fenestra for about 9 mm (Fig. 9). This extension is shorter than interpreted by Bonaparte (1971). The dorsal process contacts the lacrimal, forming a bony bar that separates the orbit from the nasoantorbital fenestra. This process is robust and tapers to a sharp point (Fig. 9). Caudally, the jugal forks into dorsocaudal and ventrocaudal processes. The former is overlain by the postorbital and takes part in the rostral margin of the infratemporal fenestra. The second partially overlies the quadrates (displaced in MHIN-UNSL-GEO-V-57).

The tetraradicate jugal of all known Pterodaustro specimens (Figs. 6, 9) differs markedly from the tri- to quadriradicate shape of the jugal of other pterodactyloids, including Pterodactylus and Anhanguera Meyer, 1851, resembling more the morphology of the jugal in some basal pterosaurs (Wellnhofer, 1991). The difference appears to be mainly on the ventrocaudal portion, where the jugal of Pterodaustro bears an extended process overlying the quadrates (Figs. 6B, 8). This contact between the quadrates and the jugal is known only for this taxon. Furthermore, Pterodaustro also differs from some derived pterodactyloids (e.g., Anhanguera, Pteranodon Marsh, 1876) in that its jugal lacks a pronounced caudodorsal ridge near the nasoantorbital fenestra.

The quadratojugal is very difficult to discern in most specimens. In MHIN-UNSL-GEO-V-57, a thin and incomplete bone, displaced ventrally to the quadrates, is tentatively identified as the left quadratojugal (Fig. 6B). According to Sanchez (1973),
this element forms all of the ventral margin of the infratemporal opening. However, such a configuration has not been observed in any other pterodactyloid (Wellnhofer, 1978).

The **quadrate** is not well preserved in any of the new specimens. This bone is rostroventrally tilted (more than 150° relative to the ventral margin of the skull; Fig. 6), a feature common to all Archaeopterodactyloidea (Kellner, 1996, 1997), as well as the Azhdarchidae (Unwin and Junchang, 1997). Rostrally, the main body of the quadrate projects mediad as a broad pterygoid flange. The proximal end of the quadrate appears to articulate with the squamosal.

The **squamosal** has an expanded, ventrolaterally rounded body (Figs. 6B, 8, 9). As shown by Sanchez (1973), this bone forms the entire ventral margin of the supratemporal fenestra (Fig. 6), restricting the postorbital to the rostral margin of this arcade. The squamosal has a thin, tapering caudomedial process that abuts the braincase (Fig. 6A). Rostroventrally, the squamosal bears a sharp, thin process that runs through the proximal half of the caudal margin of the quadrate.
Aside from the parietals, the remaining elements of the braincase appear to be completely fused, lacking discrete sutures. Yet a truncated, subtriangular bone extends laterally from the braincase in MHIN-UNSL-GEO-V-57 (Fig. 6B). This is most likely the paraoccipital process of the opisthotic. A small window between this bone and the squamosal may be the posttemporal fenestra (Fig. 6B). Although Sanchez (1973) did not identify this bone, it is very likely that the bone positioned caudoventral to the squamosal in PVL-3860 might also be the opisthotic.

Portions of the palatal bones appear in MHIN-UNSL-GEO-V-57 and MHIN-UNSL-GEO-V-135, but their compression ventral to the maxilla at the level of the nasoantorbital fenestra prevents recovering any information.

The orbit encloses a sclerotic ring. The number of plates forming the sclerotic ring is uncertain. In MHIN-UNSL-GEO-V-57, at least eight or nine plates can be distinguished (Fig. 6B). Pterosaur sclerotic rings have been reported previously, but complete sclerotic rings are known only for a handful of specimens. In Rhamphorhynchus (Meyer, 1847), sclerotic rings are formed by 13 to 15 elements and in Pterodactylus by about 20 elements (Wellnhofer,
1978). In more derived forms such as Pteranodon (Eaton, 1910; Bennett, 1991) and anhanguerids (specimen in Iwaki Coal and Fossil Museum, Japan), 12 or 13 sclerotic plates are present.

MANDIBLE

Like the snout, the mandible is curved and slender, tapering rostrally (Figs. 3, 4, 7). Most of the available information is from the lateral surface. The mandible follows the extension of the preorbital region of the skull, making the lower jaw of Pterodaustro proportionally longer than in other pterosaurs. The dentary extends almost the entire length of the mandible, and its medial dentigerous margin is higher and thicker than the lateral one. In MHIN-UNSL-GEO-V-57, for example, the dentary margin lateral to the tooth row is one-third to one-quarter shorter than the medial one.

The dentary bears teeth throughout its length (Figs. 4, 6B). This condition differs from that of other archaeopterodactyloids such as Ctenochasma, Germanodactylus, Gallovenia, and Pterodactylus, in which the dental row ends more rostrally to the caudal end of the dentary. For example, whereas Ctenochasma, Gnaurosaurus Meyer, 1834, and Pterodactylus have teeth along less than 65 percent of the mandibular length (Wellnhofer, 1978), Pterodaustro has teeth along nearly 90 percent of its mandibular length.

The region of the surangular is not well preserved in any of the new specimens and the boundary between this bone and the dentary is unclear. In MHIN-UNSL-GEO-V-57, the caudal portion of the surangular is comparatively thick, forming the rostromedial part of the articular surface for the quadrate. Toward the rostral part, the surangular appears to form a process that contributes to the dorso-caudal margin of the mandibular ramus. This process seems to end before the first mandibular tooth, where it interlocks with the dentary.

The angular is exposed laterally (Fig. 6B), but its boundaries with the surrounding bones, particularly with the articular, are difficult to interpret in the available material. Rostrally, this bone tapers under the ventral margin of the dentary. Based on MHIN-UNSL-GEO-V-57 (Fig. 6B), the dorsal extension of the angular is greater than interpreted by Sanchez (1973; Fig. 7).

The articular forms the caudal tip of the mandible (Figs. 6B, 7). This bone has a long, thin wedge underneath the angular. Unfortunately, the lateral exposure of this bone prevents recovering information about the articular facet of the mandible.

DENTITION

The upper dentition is formed by hundreds of minute teeth of equal size (Figs. 4, 10, 11). These teeth have spatulate crowns and thin, conical bases. Interestingly, the upper teeth are not set in alveoli (contra Sanchez, 1973), nor in a longitudinal groove. Instead, they are joined to the lateral surface of the recessed maxillary dentigerous margin (Figs. 10, 11). Thus, their attachment to the maxilla must have been by means of individual ligaments or, more likely, by a supporting soft-tissue structure that lined the dentigerous margin of the upper jaw. Interestingly, dorsal to most maxillary teeth, a dorso-rostrally oriented row of tiny ossicles is present, usually composed of four elements (Figs. 10, 11).

The mandibular teeth are very close to each other (Figs. 12–14). In cross section, they are oval to sub-elliptical (Chiappe and Chinsamy, 1996) and considerably thicker rostrally than in the middle and caudal sections of the mandible. The teeth are set in a groove along most of the jaw (Fig. 13), although shallow individual alveoli develop in the rostral end of the dentary (Fig. 12).

The external surface of the mandibular teeth is smooth (Figs. 13, 14). From histological sections we determined that the mandibular teeth are formed by a peripheral, thin layer of nonprismatic
enamel and an inner core of dentine surrounding a central pulp cavity (Chiappe and Chinsamy, 1996). These sections have not shown incremental lines in either the enamel or the dentine, contrary to teeth of *Anhanguera* (Chinsamy and Kellner, 1996).

### SYSTEMATIC REMARKS

The first remains of *Pterodaustro guinaizui* were all isolated specimens providing limited anatomical information about this pterosaur. A humerus (PVL-2571) was established as the holotype and a few other elements as the hypodigm (Bonaparte, 1970). On the basis of the similarity between these elements and those of *Pterodactylus*, Bonaparte (1970) assigned *Pterodaustro* to the Pterodactyliidae.

With the discovery of its peculiar skull and mandible, *Pterodaustro* was placed in its own family, Pterodaustriidae (Bonaparte, 1971), particularly because of its unique dentition and extreme extension of its preorbital region. Bonaparte (1971) considered that the Pterodaustriidae was related both to the Pterodactyliidae and the Ctenochasmatidae. Further cranial material of *Pterodaustro* was studied by Sanchez (1973), who arrived at the same conclusions as Bonaparte. The systematic relationships proposed by Bonaparte (1971) were adopted by later authors (e.g., Casamiquela and Chong-Diaz, 1980; Wellnhofer, 1991), although Wellnhofer (1978: fig. 32) considered *Pterodaustro* more closely related to *Ctenochasma*.

In a cladistic analysis of pterosaur cervical vertebral morphology, Howse (1986: figs. 11, 12) placed *Pterodaustro* in a polytomy with *Pterodactylus antiquus* Soemmerring, 1812, *Pterodactylus longicollum* Meyer, 1834, and *Ctenochasma*.
(Fig. 15). Howse (1986) correctly pointed out that all these pterosaurs have elongated midcervical vertebrae with low neural spines, although he failed to acknowledge the presence of this condition in *Germanodactylus* and *Galloboctacys suevicus* (Quenstedt, 1855).

Bennett (1994) regarded *Pterodaustro* as a basal pterodactyloid that formed a trichotomy with *Pterodactylus kochi* Wagner, 1837, and all other pterodactyloids (Fig. 15). This interpretation disagrees with all previous hypotheses by setting *Pterodaustro* apart from *Ctenochasma*, a claim that Bennett (1994) supported by citing the absence of a premaxillary sagittal crest in *Pterodaustro*. *Pterodaustro* does not have a premaxillary sagittal crest, but such a crest is also absent in several other pterodactyloids (e.g., *Galloboctacys*, *Pteranodon*, *Nuctosaurus* Marsh, 1876), which Bennett (1994) included in his grouping of all pterodactyloids other than *Pterodaustro* and *Pterodactylus kochi*. Furthermore, several characters presented by Bennett (1994) that diagnose subsequent, more exclusive nodes cannot be observed in *Pterodaustro* and are therefore equivocal, at least relative to this taxon (e.g., cervicalization of dorsal vertebrae and presence of helical jaw joint).

More recently, Kellner (1996) presented a comprehensive study of pterosaur interrelationships. This author recognized a monophyletic group, the Archaeopterodactyloidea, consisting of a clade formed by *Pterodactylus* and *Germanodactylus*, and its sister-group, an unnamed clade formed by *Ctenochasmatidae* and *Galloboctacysidae* (Fig. 15). Kellner (1996) included *Pterodaustro* within the *Ctenochasmatidae*, as the sister-taxon of *Ctenochasma* (Fig. 15). All the synapomorphies diagnosing the Archaeopterodactyloidea (e.g., rounded caudal end of the skull, resulting in a ventral displacement of the squamosal; quadrate strongly inclined caudally, with an angle of about 150° relative to the ventral margin of the skull; elongated midcervical vertebrae; neural spines of the midcervical vertebrae low and bladelike; see Kellner, 1996, 1997) are present in *Pterodaustro*.

In Kellner's analysis, the close relationship of *Pterodaustro* and *Ctenochasma* is supported by a single synapomorphy: the presence of a large number of teeth (more than 150; Kellner, 1996, 1997). However, the rostral extension of the surangular of *Pterodaustro* and *Ctenochasma* is smaller than that of other archaeopterodactyloids and may be another synapomorphy of these taxa.

A close relationship between *Pterodaustro* and *Ctenochasma* was also recently supported by Unwin and Junchang (1997), who included these and other Late Jurassic–Early Cretaceous pterosaurs (e.g., *Gnathosaurus*, *Huanhepterus* Dong, 1982; *Cearadactylus* Leonardi and Borgomano, 1985) within the *Ctenochasmatidae* (Fig. 15). However, these authors did not mention any specific synapomorphy uniting these taxa but simply pointed to the filter-feeding specializations usually inferred for them. In contrast to Kellner's (1996) hypothesis, Unwin and Junchang (1997) considered the *Ctenochasmatidae* to be the sister-group of *Pterodactylus*, regarding *Galloboctacys* as a more basal member of the *Ctenochasmatidae*—the higher taxon used by Unwin and Junchang (1997) to group *Ctenochasmatidae*, *Pterodactylus*, and *Galloboctacys*. Unfortunately, these authors did not provide evidence for the proposed relationships within their *Ctenochasmatidae*.

However, support for the sister-group relationship of *Ctenochasmatidae* and *Galloboctacidae* is provided by the presence of a concave dorsal margin of the skull (Kellner, 1996, 1997). In all other pterosaurs, the dorsal margin of the skull is either straight or convex. According to the reconstruction presented by Bennett (1991), the dorsal margin of the skull in *Pteranodon* is also concave. However, it must be noted that few complete skulls are known and that in some of these the dorsal margin is essentially straight (Bennett, 1994: fig. 1). If the dorsal margin of the skull of *Pteranodon* was indeed concave, it is probable that this condition was achieved independently (Kellner, 1996).

Kellner (1996) diagnosed the monophyletic group formed by *Pterodactylus* and *Germanodactylus* on the basis of their particular dentition (more than 15 peglike teeth) and the presence of a straight lateral process of the nasal that is not connected to the maxilla. MHIN-UNSL-GEÖ-V-57 has a straight lateral process of the nasal, suggesting that this apomorphic character may be a synapomorphy of a more inclusive clade, most likely the Archaeopterodactyloidea. Because this process is very delicate, its supposed absence in *Galloboctacys* and *Ctenochasma* (Kellner, 1996) may result from preservational factors.

The skull of *Pterodaustro* exhibits numerous characters of its own that are clear autapomorphies of this taxon. The most obvious are in the dentition. The spatulate teeth of the maxilla of *Pterodaustro* differ from those of all other pterosaurs (Bonaparte, 1971; Sanchez, 1973). In addition, the fact that the maxillary teeth are not set in alveoli and that they are associated with a row of ossicles are other autapomorphic characters. Another distinct autapomorphy of *Pterodaustro* is the remarkable extension of its preorbital region, which is not known in other pterosaurs (Bonaparte, 1971; Sanchez, 1973). As a consequence of this preorbital

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Figure 13 Stereoelectronmicrograph of the mandibular teeth of *Pterodaustro guinauzi* (MHIN-UNSL-GEÖ-V-57) showing their insertion in a dentary groove with lower (A) and higher (B) magnification. In A and B, scale bars equal 2 and 1 millimeters, respectively.
extension, the nasoantorbital fenestra of *Pterodaustro* occupies only 10–12 percent of the total length of the skull. In contrast, the nasoantorbital fenestra constitutes 15–16 percent of the length of the skull in *Ctenochasma* and 18–19 percent in *Pteranodon* (excluding the cranial crest; see Bennett, 1991: fig. 2).

Furthermore, unlike any other pterosaur, in *Pterodaustro* the postorbital is separated from the frontal, and the quadrate-jugal appears to form the ventral margin of the infratemporal opening (Sanchez, 1973), which in other pterodactyloids is mostly formed by the quadrate (e.g., *Pterodactylus*; Wellnhofer, 1978). Besides, the presence of four jugal processes in *Pterodaustro* may be another autapomorphy. In all pterodactyloids for which the jugal is known, the caudoventral region of this bone is rounded and does not form an independent process. The apparent contact between the jugal and the quadrate on the lateral surface of the skull (Bonaparte, 1971; Sanchez, 1973) is another potential autapomorphy of *Pterodaustro*, because this feature is not known for other pterodactyloids.

The mandible of *Pterodaustro* also displays several autapomorphic features. The large number of teeth (nearly 500 for each ramus) and their filamentialike aspect are unique among pterosaurs. Also, the extensive length of the mandible, which follows the extension of the preorbital region of the skull, is another autapomorphy of *Pterodaustro*. This condition differs from that in all other pterosaurs, including *Pteranodon*, in which the elongation of the preorbital region is not matched by the lower jaw, which is considerably shorter (Bennett, 1991).
Figure 15 Different phylogenetic hypotheses of the relationships of *Pterodaustro guinauzi* to other pterodactyloids

In sum, although the skull and jaws of *Pterodaustro* are easily distinguishable from those of other pterosaurs by a large number of autapomorphic features, two derived cranial characters (i.e., more than 150 teeth and a reduced rostral projection of the surangular) support the close relationship to *Ctenochasma* advocated by most authors.

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