

Early juvenile pterosaurs (*Pterodactyloidea*: *Pterodaustro guinazui*) from the Lower Cretaceous of central Argentina

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Abstract: We report on two juvenile specimens of *Pterodaustro guinazui*, a medium-sized, filter-feeding pterodactyloid pterosaur from the Lower Cretaceous (Albian) lacustrine deposits of the Lagarcito Formation of central Argentina (Sierra de Las Quijadas, San Luis Province). Both specimens lack the skull, but one is otherwise nearly complete and articulated, and the other is more fragmentary. Their small size (~300 mm of wingspan), the lack of fusion of several postcranial bones, the minimal epiphyseal ossification, and the porous appearance of the periosteal surfaces indicate the specimens died at a very early stage of postnatal development. The presence of derived characters unique, within Pterodactyloidea, to *P. guinazui* (e.g., caudal vertebrae exceeding 16 elements) supports the proposed specific identification of the specimens. The new material provides anatomical information previously unknown for *P. guinazui* and sheds light on allometric transformations during the growth of this pterosaur. Comparisons with more mature and much larger individuals support two major allometric trends: (i) the negative allometric growth of the proximal portion of the forelimb, and (ii) the positive allometric growth of the metacarpal IV.

Résumé : Nous soumettons un article sur deux spécimens juvéniles de *Pterodaustro guinazui*, un ptérosaure ptérodactyloïde, de taille moyenne et qui se nourrit par filtrage, dans les dépôts lacustres de la Formation de Lagarcito (Crétacé inférieur – Albien) du centre de l'Argentine (Sierra de Las Quijadas, province de San Luis). Aucun des deux spécimens n'a de crâne mais l'un des deux est presque complet et articulé alors que l'autre est plus fragmenté. Leur petite taille (envergure ~ 300 mm), le manque de fusion de plusieurs os postcrâniens, l'ossification épiphysaire minimale et l'apparence poreuse des surfaces du périoste indiquent que les spécimens sont morts à un stage très précoce de développement postnatal. La présence de caractères dérivés, uniques à *Pterodaustro guinazui* chez les ptérodactylidés, (p. ex. des vertèbres caudales à plus de 16 éléments) supporte l'identification spécifique proposée des spécimens. Le nouveau matériel fournit de l'information anatomique auparavant inconnue pour *Pterodaustro guinazui* et nous renseigne sur les transformations allométriques au cours de la croissance de ce ptérosaure. Des comparaisons avec des individus plus adultes et beaucoup plus grands supportent deux tendances allométriques majeures : (1) la croissance allométrique négative de la portion proximale du membre antérieur et (2) la croissance allométrique positive du 4^e métacarpien.

[Traduit par la Rédaction]

Introduction

At “Loma del *Pterodaustro*” (32°29.65'S, 66°59.38'W; Fig. 1), a site of the Lower Cretaceous (Albian) Lagarcito Formation in the northwestern corner of the Argentine province of San Luis (Fig. 1) (Chiappe et al. 1998a, 1998b, 2000), hundreds of specimens of the filter-feeding pterodactyloid *Pterodaustro guinazui* have been collected since the site was first excavated in the late 1960s (Bonaparte 1970, 1971). Among these are two small specimens (MHIN-UNSL-GEO-V 241 and MMP 1168) that represent very early stages of postnatal development. These fossils not only add to the poor record of pterosaur

specimens that represent early life history stages, but also provide evidence of allometric changes during the postnatal development of *Pterodaustro* and contribute to our knowledge of the anatomy (Sanchez 1973; Chiappe et al. 2000) of this spectacular ctenochasmatid pterodactyloid.

Institutional abbreviations

MHIN-UNSL-GEO-V, Museo de Historia Natural de la 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.

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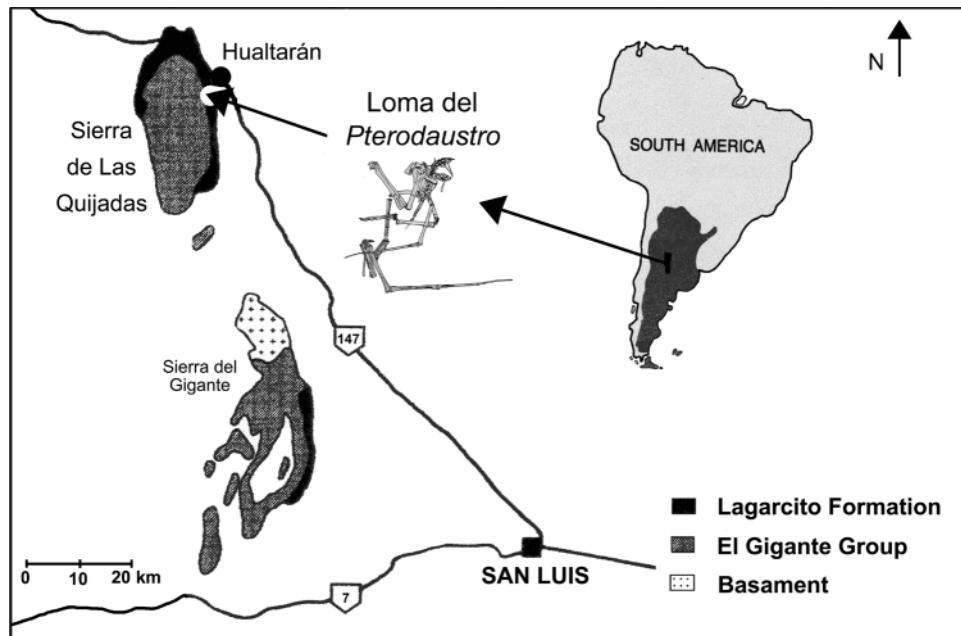
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Fig. 1. Geographic distribution of the Lagarcito Formation and location of the Loma del *Pterodaustro* fossil site.



Material

MHIN-UNSL-GEO-V 241 (from here on referred to as V 241) and MMP 1168 were collected as split slab and counterslab, although the two slabs of V 241 were put together during preparation. V 241 constitutes a nearly complete specimen, whose wingspan approaches 280 mm (Table 1) and includes most of the vertebral column (cervical series missing), a few thoracic ribs, portions of the pectoral and pelvic girdles, a complete right wing, portions of the left wing, and both hindlimbs (Fig. 2). The proximal portion of the right wing (humerus, radius, and ulna) has rotated 180° and is exposed in ventral view on the left side of the specimen. The hand of this forelimb is detached from these elements and is displaced on top of the left foot. The right hand is essentially exposed in dorsal view, with the fourth metacarpal rotated somewhat caudally. The incomplete left fourth digit (the only preserved portion of the left forelimb) is also exposed in dorsal view and spread over the right hindlimb, left foot, and right hand. The left hindlimb is exposed cranio-laterally, with the pes in cranial view. The right hindlimb is exposed in caudomedial view. MMP 1168 (Fig. 3) is slightly larger than V 241, with an estimated wingspan of 300 mm (Table 1). MMP 1168 preserves much of a forelimb and a hindlimb and the caudal series. The forelimb (possibly the left one) includes the humerus, impressions of portions of the radius and ulna, and the wingfinger, of which phalanges 3 and 4 are nearly complete. The hindlimb (apparently the left one) includes portions of the femur, tibia, tarsals, and the complete foot.

Description

The following description is primarily based on V 241, the more complete and better preserved of the two specimens.

Axial skeleton

The vertebral column of V 241 is articulated from the caudal series to the rostral portion of the dorsal series. Seven

Table 1. Selected measurements (maximum lengths in mm) of specimens MHIN-UNSL-GEO-V 241 and MMP 1168.

	MHIN-UNSL-GEO-V 241		MMP 1168
	Left	Right	
Humerus	19.23	—	22.75 ^a
Radius	24.84	—	—
Ulna	24.87	—	—
Metacarpal I	12.50 ^a	—	—
Metacarpal IV	16.80	—	—
F1d4	25.20	—	—
F2d4	22.79	—	—
F3d4	18.44	18.49	20.37
F4d4	17.58	17.66	17.55 ^a
Ilium	8.89 ^a	8.96 ^a	—
Femur	14.23 ^a	13.14 ^a	14.08 ^a
Tibia	19.73 ^a	18.85	—

Note: F1d4–F4d4, first to fourth phalanges of the wingfinger.

^aEstimated.

dorsal ribs are preserved, five of which are in articulation with the vertebrae. The tail, sacrum, and caudalmost dorsal vertebrae are exposed dorsally; the more cranially positioned dorsal vertebrae gradually rotate laterally.

The dorsal series appears to be composed of 14–15 vertebrae. In at least the cranialmost vertebrae of the series, the neural arches are separated from their respective centra. All dorsal vertebrae are similar in shape. Their centra are subquadrangular in lateral view, and their neural arches lack pneumatic foramina.

The number of sacral vertebrae is uncertain. In V 241, one or two additional elements could have been present in addition to the four well-preserved vertebrae composing the cranial half of the sacrum (Fig. 4). The centra of these vertebrae are

fused to one another, but the transverse processes and neural spines remain unfused. The first sacral just contacts the ilium. Its left transverse process is well preserved, showing that it was angled at 45° posteriorward with respect to the axis of the sacrum. The transverse processes of the following two vertebrae are smaller and they project nearly perpendicularly from the sacrum.

The caudal series of MMP 1168 (Fig. 3) is more completely preserved than that of V 241. Whereas in V 241 only the most proximal 10 caudals have been preserved, MMP 1168 preserves 21–22 caudals, and it seems that the tail is not entirely complete. Caudal vertebrae lack transverse processes. The first nine vertebrae have subquadrangular centra. Subsequent vertebrae have more subrectangular centra. The caudals reach their maximum length at about the 10th vertebra, and they then decrease in length towards the distal end of the tail. The shape of these vertebrae and the relative lengths across the tail are comparable to those of MHIN-UNSL-GEO-V 243, a subadult specimen of *P. guinazui* preserving 22 caudal vertebrae. The only appreciable difference between MHIN-UNSL-GEO-V 243 and MMP 1168 or V 241 is the greater ossification of the vertebrae and the fact that the neural spine of one element overlaps the preceding centrum.

Appendicular skeleton

Pectoral girdle and forelimb

Of the pectoral girdle, only the distal end of a scapula and corresponding coracoid of V 241 are preserved. Whether these correspond to the right or left side is uncertain, although their proximity to the proximal end of the right humerus suggests these elements constitute the right pectoral girdle. Little about these elements can be evidenced beyond the fact that, unlike in adult individuals, the elements are not fused to one another.

The humerus of the juveniles (Fig. 4) presents the primitive pterodactyloid condition of a short (~23% of the humeral length in V 241), rounded, and somewhat ventrally curved deltopectoral crest that is parallel to the shaft. Although the relative length of the deltopectoral crest increases with an increase in the size of the humerus (e.g., in MHIN-UNSL-GEO-V 163 it is 30% of the length of the 135 mm long humerus), its relative size approaches more that of dsungaropterids and basal pterodactyloids than that of the much longer (~40% of the humerus) and warped deltopectoral crest of *Pteranodon* and other ornithocheiroids (Bennett 1989, 1994, 2001; Unwin 1995).

In both juvenile specimens, the shaft of the humerus is straight and its diameter remains essentially constant throughout its length. This condition is likely the result of the lack of ossification of the distal end, thus giving the humerus its uniform width. The straight shaft of the humerus differs from that of *Pterodactylus*, *Gallodactylus*, and *Rhamphorhynchus* where it is somewhat curved (Bennett 1994). The humerus is also curved in "*Pterodactylus elegans*," which Bennett (1993, 1996) interpreted as a juvenile of *Ctenochasma gracile* (see also Unwin 1995). The straight condition of the humeral shaft is similar to that of subadult and adult specimens of *P. guinazui* (e.g., MHIN-UNSL-GEO-V 243, MHIN-UNSL-GEO-V 95, MMP 1177). In these more mature individuals of *Pterodaustro*, however, the diameter of the shaft remains uniform over the proximal two thirds then increases in width

over the distal third. This seemingly primitive condition differs from that of ornithocheiroids, where the diameter of the shaft increases from the base of the deltopectoral crest distalwards (Bennett 1989).

The right radius and ulna of V 241 are nearly complete and exposed in dorsolateral view. These bones are straight, with shafts of almost the same width (that of the ulna is only slightly wider). The ulna appears to lack pneumatic foramina. The distal condyles of the ulna are barely ossified. The proximal end of the radius bears a tubercle, possibly for the ligamental attachment of the bicipital musculature.

Two poorly ossified elements are preserved in the carpus. Metacarpal I seems to be of the same length as metacarpal IV, but because the proximal portion is covered by metacarpal IV, it is uncertain whether or not it articulated with the carpus. In dorsal view, the slender metacarpal I is straight. Another metacarpal, corresponding to either metacarpal II or metacarpal III, is somewhat displaced from its original position, with its distal end covered by metacarpals I and IV. Nonetheless, its length seems to be comparable with that of metacarpal I. The right hand of V 241 is well preserved and includes the four phalanges of the wingfinger (F1d4–F4d4) and the nearly complete digits I–III. Assuming that the phalangeal formula of the latter digits is comparable to the 2–3–4 formula of other pterosaurs (Wellnhofer 1970, 1991), only the ungual phalanx of digit II is missing (Fig. 5). Interestingly, the second and third (intermediate) phalanges of digit III are subequal in length. This condition drastically differs from that present in adult specimens of *Pterodaustro* (e.g., MHIN-UNSL-GEO-V 243), *Pterodactylus* (e.g., *P. antiquus* and *P. kochi*), *Haopterus gracilis*, *Anhanguera piscator*, *Pteranodon*, and other pterodactyloids (e.g., Wellnhofer 1970, 1978; Kellner and Tomida 2000; Bennett 2001; Wang and Lü 2001), in which the third phalanx is much longer. Nonetheless, the condition in V 241 approaches that of juvenile specimens of *C. gracile*, such as that described as "*Pterodactylus elegans*" (Bennett 1993, 1996). Perhaps more important for the taxonomic identification of the specimens reported here is the presence of a proximal phalanx of digit II that is longer than the intermediate phalanx of this digit. Although this phalangeal proportion opposes the typical condition of pterodactyloids (D.M. Unwin, personal communication), it agrees with that present in *Pterodaustro* (MHIN-UNSL-GEO-V 243) and *Ctenochasma* (de Buissonjé 1981).

The right metacarpal IV is viewed in dorsocaudal view. As in all other pterosaurs, this bone is much more robust than the other metacarpals. No articulation for the distal syncarpal or pneumatic foramen is visible. The first three phalanges of this wingfinger are straight, and the last one is slightly curved. In V 241, the extensor tendon process of the first phalanx (F1d4) is not fused to the phalangeal shaft. This process, however, is completely fused to the phalangeal shaft in adult specimens of *Pterodaustro* (MHIN-UNSL-GEO-V 147, MMP 1034, MHIN-UNSL-GEO-V 252). Based on V 241, the phalangeal proportions of digit IV (1.00:0.90:0.73:0.69) are similar to those of the more mature specimens of *Pterodaustro* (1.00:0.94:0.73:0.58 in MHIN-UNSL-GEO-V 243; 1.00:0.90:0.69:0.54 in PVL 3860).

Pelvic girdle and hindlimb

Only portions of the ilia are preserved in V 241; the pelvis

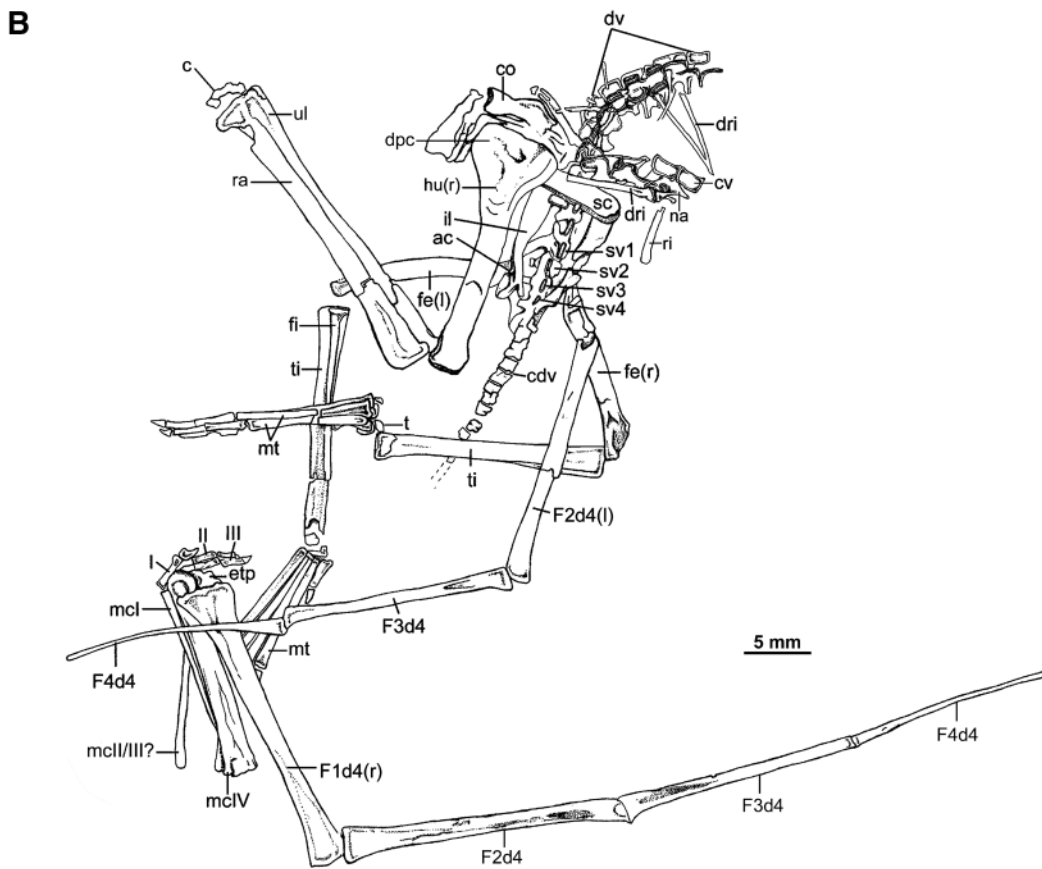
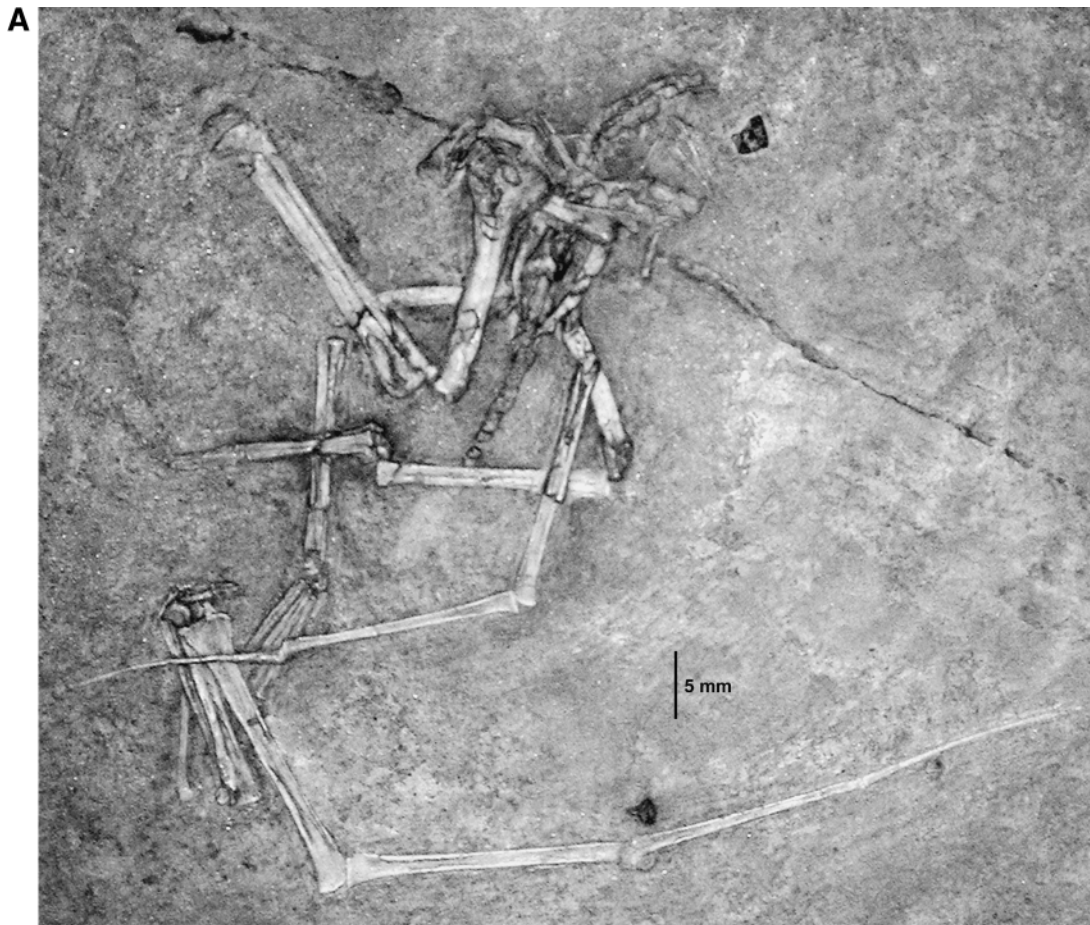
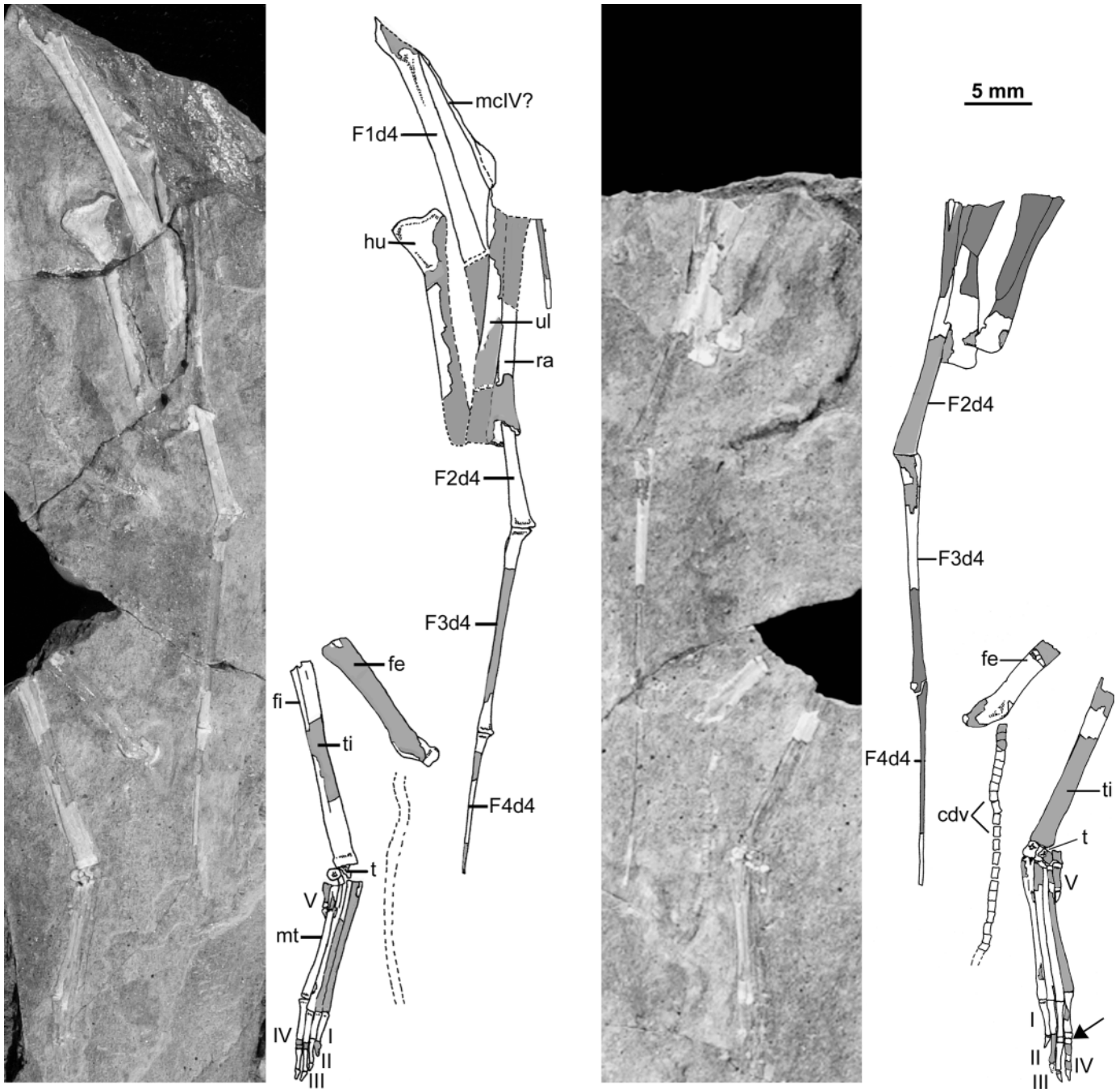


Fig. 2. (A) Photograph of specimen MHIN-UNSL-GEO-V 241. (B) Interpretive drawing of MHIN-UNSL-GEO-V 241. ac, acetabulum; c, carpals; cdv, caudal vertebrae; co, coracoid; cv, vertebral centrum; dpc, deltopectoral crest of the humerus; dri, dorsal rib; dv, dorsal vertebrae; etp, extensor tendon process; fe, femur; fi, fibula; F1d4, first phalanx of the wingfinger; F2d4, second phalanx of the wingfinger; F3d4, third phalanx of the wingfinger; F4d4, fourth phalanx of the wingfinger; hu, humerus; il, ilium; (l), left; mclI, metacarpal I; mclII/III?, metacarpal II or III; mclIV, metacarpal IV; mt, metatarsals; na, neural arch; (r), right; ra, radius; ri, rib; sc, scapula; sv, sacral vertebrae; t, tarsal; ti, tibia; ul, ulna.

Fig. 3. Photograph and interpretive drawing of specimen MMP 1068 (slab, left; counterslab, right). Note the intermediate phalanges of digits III and IV (arrow) and the single phalanx of digit V visible on the counterslab. I–V, pedal digits. Other abbreviations as in Fig. 2.



of MMP 1168 is completely missing. The ilium has a long and flat preacetabular wing and a shorter postacetabular process. The femur has a curved shaft and a short neck. The tibia is long and straight, and, as shown by MMP 1168, its distal

end is still not fused with the astragalus and calcaneum. The fibula seems to be a little less than two thirds of the length of the tibia. MMP 1168 also preserves the impression of the lateral distal tarsal, which remains in articulation with metatarsal

Fig. 4. Detail of the sacral and caudal vertebrae of MHIN-UNSL-GEO-V 241. ns, neural spine; sv1, first sacral vertebrae; tp, transverse process.

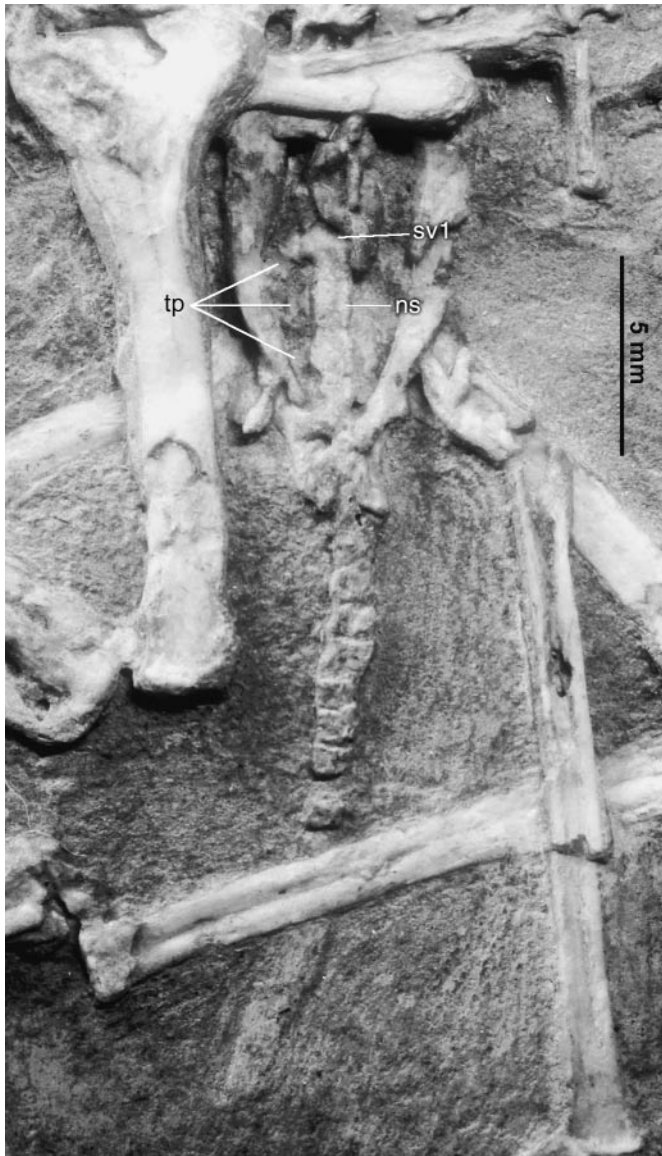
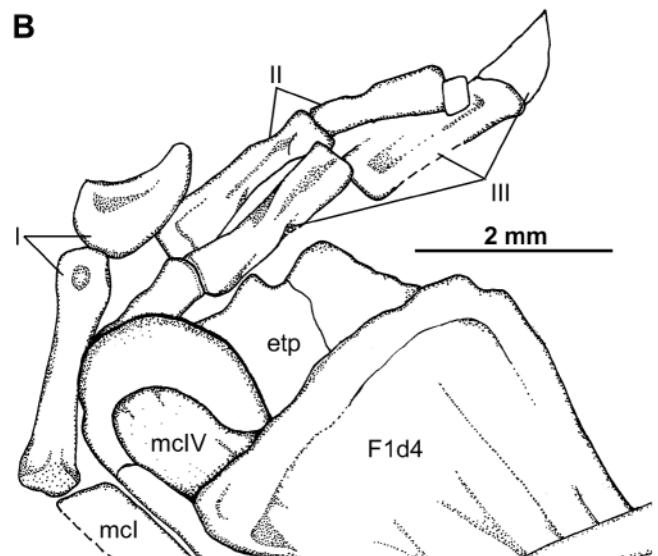
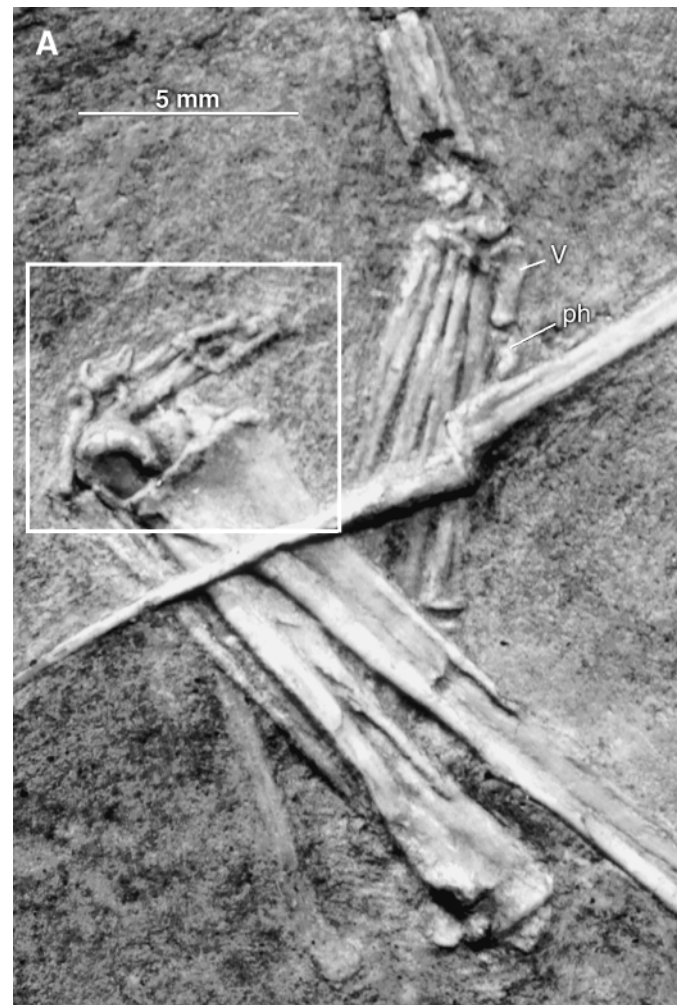


Fig. 5. (A) Details of right hand and foot of MHIN-UNSL-GEO-V 241. (B) Drawing of area within the box in (A). ph, phalanx of pedal digit V; I–III, manus digits I–III; V, pedal digit V. Other abbreviations as in Fig. 2.



V. The foot bears five digits, albeit the short digit V accounts for only 20% of its length. Metatarsals I–IV are straight and slender; their proximal ends are expanded and spatula-shaped. Metatarsal III is the longest. MMP 1168 reveals a phalangeal formula of 2–3–4–5–1. Despite the immaturity of this specimen, the pterodactyloid condition of short intermediate phalanges in digits III and IV is clearly visible. The presence of a single phalanx on digit V, a primitive pterodactyloid condition (Bakhurina 1992), was previously unknown for *Pterodaustro* (Figs. 3, 5). Metatarsal V is straight and only slightly expanded proximally, a condition similar to that of other basal pterodactyloids. As in other specimens of *Pterodaustro*, the ungual phalanges of the early juveniles are nearly straight and lack prominent flexor tubercles, a design that contrasts with the sharp unguals of *Pterodactylus*, which bear pronounced flexor tubercles.

Discussion

The two specimens reported here are virtually identical in every aspect for which their preservation permits comparisons. These morphological similarities are particularly evident in the humerus, caudal vertebrae, and pes. V 241 and MMP 1168 also show the same ratios between elements of both the forelimb and the hindlimb. These similarities and the absence of any significant differences suggest that V 241 and MMP 1168 belong to the same taxon.

All diagnosable pterosaur material collected so far from the Loma del *Pterodaustro* appears to belong to the ctenochasmatoid *P. guinazui*, which cladistic analyses have generally included within the Ctenochasmatidae (e.g., Unwin 1995, 2002; Kellner 1996; Chiappe et al. 2000; Unwin et al. 2000). The general morphology of V 241 and MMP 1168 compares well with that of the adult and subadult specimens of *Pterodaustro*. V 241 resembles *Pterodaustro* and other ctenochasmatids in the proportions of the non-ungual phalanges of manual digit II, the relative length of the ulna and femur (ulna/femur = 1.70), and the relative length of the tibia and metatarsal III (tibia/metatarsal III) = 1.74 (Unwin et al. 2000). In addition, when the ulna/femur and tibia/metatarsal III ratios of V 241 are plotted against the length of the wing phalanx 1 (F1d4) and the femur, respectively, the resultant values are nested within those of ctenochasmatids (Unwin et al. 2000, fig. 6). Furthermore, the relative ratios of the wing phalanges also approximate those of *Pterodaustro*, although these ratios are not distinguishable from those of other ctenochasmatoids.

Perhaps the most important similarities for supporting the taxonomic assignment of the early juveniles to *P. guinazui* are in the tail. Within Pterodactyloidea, and in particular within Ctenochasmatidae, the number and morphology of the caudal vertebrae are not known in great detail: most of the eight species usually included within Ctenochasmatidae are known on the basis of cranial material. Nonetheless, several specimens of *Pterodaustro* (e.g., MHIN-UNSL-GEO-V 165, MHIN-UNSL-GEO-V 243, MMP 1168, V 241) preserve portions of the caudal series. Caudal information for other ctenochasmatids is limited to only two specimens of *C. gracile* (Opper 1862; Broili 1936) and one of *Huanepiterus quingyangensis* (Dong 1982), and the anatomical details of these vertebrae have not been described. Based on subadult specimens (e.g., V 243), the caudal series of *Pterodaustro* contains more than 22 vertebrae. By contrast, the caudal series in *C. gracile* consists of fewer vertebrae, and the impression of just two caudals in *Huanepiterus* also suggests a shorter tail for this taxon (Dong 1982). Indeed, the number of vertebrae in the tail of *Pterodaustro* seems to be substantially greater than that for any other pterodactyloid. Within Pterodactyloidea, *Pterodactylus* (at least *P. antiquus*) has 16 simple, amphiplatyan vertebrae (Bennett 1991, 2001), and in more advanced pterodactyloids such as *Anhanguera* (Kellner and Tomida 2000) and *Pteranodon* (Bennett 2001) the number of caudals is limited to only 11. The relative length of the tail of *Pterodaustro* also appears to be substantially greater than that of any other pterodactyloid. Although the tail length of most pterodactyloids ranges from between 2.5% and 4.2% of the length of the wingspan (e.g., *Pterodactylus*, *Pteranodon*, *Nyctosaurus*, *Dsungaripterus*) (Bennett 1987, 2001), it is 5.2% of the length of the wingspan in V 241 and nearly 7%

in MHIN-UNSL-GEO-V 243. Pterosaurs primitively have long tails with a much greater number of caudal vertebrae (Wellnhofer 1975, 1991; Wild 1978; Dalla Vecchia et al. 2002). The observation, however, that the caudal series of *Pterodaustro* contains many more elements than that of any other pterodactyloid should not necessarily indicate that *Pterodaustro* retains the primitive condition. Most importantly, phylogenetic studies have consistently shown that *Pterodaustro* is nested deep within Unwin's (1995) Ctenochasmatoidea, or Kellner's (1996) Archaeopterodactyloidea (see also Chiappe et al. 2000), indicating that the increased number of caudal vertebrae in this pterosaur is not a primitive but a derived condition. Thus, the presence of caudal counts exceeding 22 vertebrae in the immature specimens described here and in specimens of *P. guinazui* (e.g., MHIN-UNSL-GEO-V 243) constitutes an autapomorphy supporting the identification of V 241 and MMP 1168 as early juveniles of this pterodactyloid species. In addition, the relative lengths of caudal vertebrae and morphological transition that they show within the tail of these specimens also support this taxonomic hypothesis. In *Pterodaustro* (e.g., MHIN-UNSL-GEO-V 243), caudal vertebrae reach their maximum length more distally than in other pterodactyloids (e.g., *Anhanguera*, *Pteranodon*) and at about the same position (caudal vertebrae 9–10) as in MMP 1168. The straight condition of the humeral shaft of the early juveniles also resembles the condition of adults of *P. guinazui*. The fact that other ctenochasmatoids (e.g., *Pterodactylus*, *Gallodactylus*, *Ctenochasma*) and *Rhamphorhynchus* have a somewhat curved shaft suggests that the straight condition may also be an autapomorphy of *P. guinazui*. This statement, however, needs to be further examined.

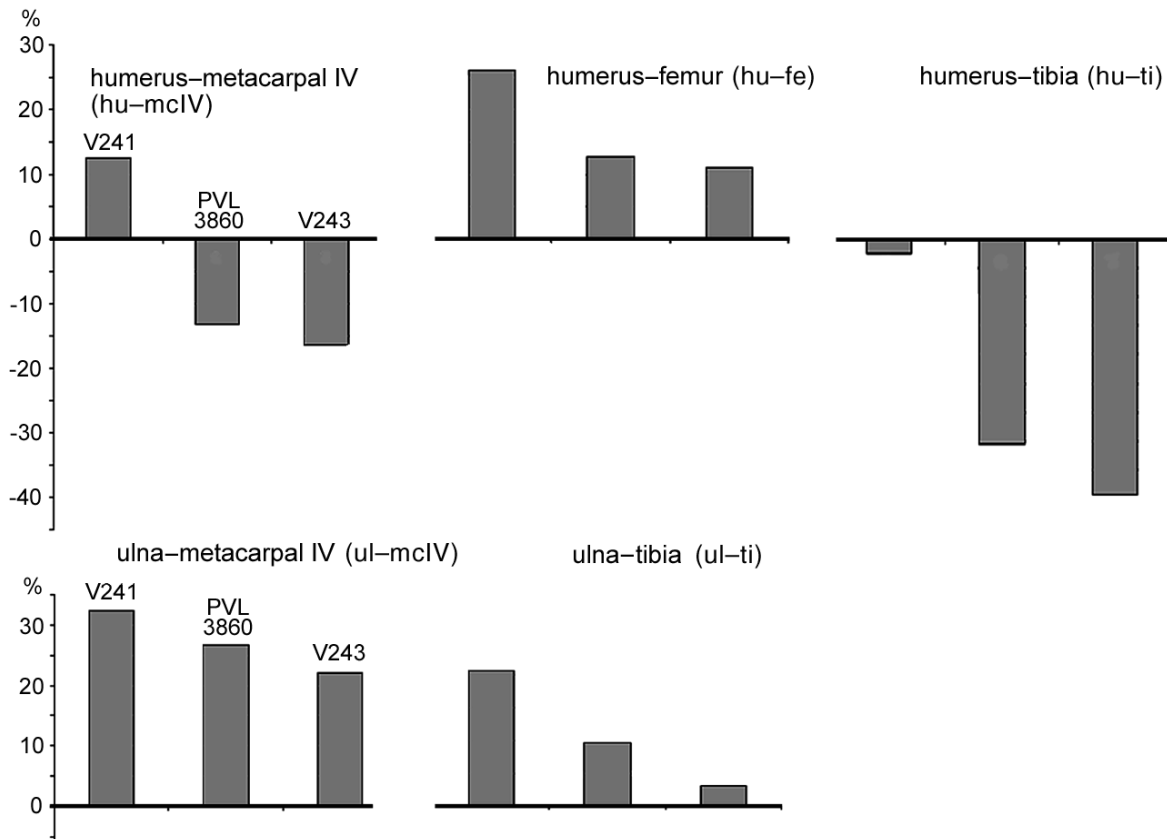
Early juvenile characters

In addition to their small size, V 241 and MMP 1068 exhibit several morphological features indicating that these individuals died at a very early stage of postnatal development (Bennett 1993; Wild 1993). The most salient of these features are (i) the absence of fusion between vertebral centra and neural arches (at least in the anterior dorsal series of V 241); (ii) the incomplete fusion of the sacrum, in which the transverse processes and neural spines remain unfused to each other (preserved only in V 241); (iii) the lack of ossification of the humeral condyles (visible only in V 241); (iv) the lack of fusion between the scapula and coracoid (preserved only in V 241); (v) the lack of fusion between the proximal articulation of the first phalanx of the wingfinger and the extensor tendon process (also only preserved in V 241); and (vi) the lack of fusion between the proximal tarsals and the tibia. In addition, most bones of these specimens are poorly ossified and their periosteum exhibits the porous appearance typical of early juvenile archosaurs (Bennett 1993; Sanz et al. 1997; Horner 2000; Ricqlès et al. 2000).

Allometric changes

At least five significant allometric transformations (Fig. 6) can be observed when the early juveniles described here are compared to subadult and adult individuals of *P. guinazui*: (i) whereas the early juvenile humerus is some 12.6% longer than the metacarpal IV, in the subadult the humerus is signif-

Fig. 6. Relative lengths of various elements expressed as a percentage of longer (+) or shorter (-) values for MHIN-UNSL-GEO-V 241 and two more mature specimens of *Pterodaustro guinazui* (PVL 3860, MHIN-UNSL-GEO-V 243) of different sizes (as indicated by their wingspans). ws, wingspan. Other abbreviations as in Fig. 2.



	hu-mcIV	hu-fe	hu-ti	ul-mcIV	ul-ti
V241 (ws=289 mm)	(+)12.6%	(+)26.0%	(-)2.6%	(+)32.4%	(+)20.6%
PVL3860 (ws=1276 mm)	(-)13.3%	(+)12.8%	(-)35.8%	(+)26.7%	(+)9.7%
V243 (ws=1590 mm)	(-)16.3%	(+)11.1%	(-)44.5%	(+)22.0%	(+)3.1%

icantly shorter than this metacarpal (13.3% and 16.3% shorter in PVL 3860 and in the larger MHIN-UNSL-GEO-V 243, respectively); (ii) in the early juveniles the humerus is 26% longer than the femur, but in subadults the humerus is only 12.8% (PVL 3860) or 11.1% (MHIN-UNSL-GEO-V 243) longer than the femur; (iii) the humerus and tibia are subequal in length in the early juveniles, but the former bone is 35.8% and 44.5% shorter than the latter in PVL3860 and the larger MHIN-UNSL-GEO-V 243, respectively; (iv) in the early juveniles the ulna and radius are 32.4% longer than the metacarpal IV but only 26.7% (PVL 3860) or 22% (MHIN-UNSL-GEO-V 243) longer in subadult specimens; and (v) in the early juveniles the ulna is also 20.6% longer than the tibia but only 9.7% longer in PVL 3860 and subequal (3.1% longer) in the larger MHIN-UNSL-GEO-V 243. In addition, changes in the proportions of the phalanges of the wing-finger also reveal allometric growth patterns. Although the relative lengths of the two intermediate phalanges of this

digit remain constant between early juveniles and mature individuals, the relative length of the fourth phalanx (F4d4) with respect to that of the proximal phalanx (F1d4) is approximately 10% greater in the early juveniles, thus F4d4 is relatively shorter in adults.

The variation in relative proportions (Fig. 6) suggests that growth in *P. guinazui* was characterized by two major allometric patterns: negative allometry in the proximal portion of the forelimb (humerus and ulna-radius), and positive allometry of the metacarpal IV. Some of these observations compare well with those reported by Mateer (1976), who applied multivariate techniques to measurements published by Wellnhofer (1970) for *Pterodactylus*. Consistent with the interpretations proposed by Wellnhofer, Mateer demonstrated that during the ontogeny of *Pterodactylus micronyx* the distal portion of the wing grew with positive allometry and that F3d4 and F4d4 suffered negative allometry with respect to the other phalanges of the wingfinger. Thus, the allometric

pattern in *P. micronyx* resembles that inferred here for *P. guinazui*, although in the latter species the growth of F3d4 appears to be isometric.

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