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MIDDLE MIOCENE CROCODILES FROM THE FITZCARRALD ARCH, AMAZONIAN PERU

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INTRODUCTION

Hyperdiversity of tropical Neogene crocodiles in South America is unquestionable. The great variety of crocodile taxa has been related with environmental conditions similar to the marine–like megalake Pebas proposed by Wesselingh *et al*. (2002) for western Amazonia (Cozzuol, 2006). However, our knowledge of most taxa is supported by insufficient material of a small number of remarkable localities like La Venta (Middle Miocene, Colombia; Langston, 1965; Langston and Gasparini, 1997), Acre (Late Miocene, Brazil; Cozzuol, 2006) and Urumaco (Late Miocene, Venezuela; Sánchez-Villagra and Aguilera, 2006).

Two recent expeditions to the Fitzcarrald Arch in Amazonian Peru discovered and collected numerous stratigraphically in situ vertebrate remains referred as a whole to the late Middle Miocene (Salas-Gismondi *et al*., 2006; Antoine *et al*., this volume). The Fitzcarrald Arch uplift –no older than Pliocene– is due to the Nazca Ridge subduction (Espurt *et al*., 2007), and corresponds to widespread dissected reliefs of middle Miocene sediments equivalent to the more northern Pebas deposits. The Inuya-Mapuya sites are located in the poor deformed part of the Fitzcarrald Arch. They correspond to outcrops of the Amazon foreland strata with tidal facies attesting the presence of Middle Miocene giant estuaries alimented by Andean rivers. Bones are located in conglomerates of clay pebbles, which probably cap transgressive surfaces of erosion (Espurt *et al*., 2006). The Alto Urubamba sites are located in the thrust deformed zone (Subandean zone) of the Fitzcarrald Arch, near the Camisea anticline. Middle Miocene Subandean outcrops in this area (Pebas equivalent) show continental facies related to the incipient reliefs of the Eastern Andes. In Alto Urubamba sites, vertebrate remains were found in channel conglomerates.

Institutional Abbreviations: MRU, Museo Regional de Ucayali, Perú; MUSM, Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Perú.

CROCODILES FROM FITZCARRALD (INUYA-MAPUYA AND ALTO URUBAMBA LOCALITIES)

The crocodile fauna (Fig. 1) is represented at least by eight different taxa referable to the ziphodont Sebecosuchia (Sebecidae) and Eusuchia (Gavialidae, Nettosuchidae, and Alligatoridae). Ziphodont crocodiles are particularly interesting since two types are recognized. Buffetaut and Hoffstetter (1977) referred a partial snout of a big oreinirostral crocodile found in Mapuya River to *Sebecus* cf. *huilensis*, a species previously known only from La Venta (Fig. 1 A). Subsequent studies based on new material rejected initial assignment and relations with Bretesuchids were suggested (Busbey, 1986; Langston and Gasparini, 1997). Although, this specimen is definitely distinct from *S. huilensis*, we retain it in the Sebecidae due to laterally compressed teeth, not broadening of the rostrum at level of fifth maxillary alveoli, and straight premaxilla. It might represent a new giant species of uncertain affinities. On the other hand, our survey at the Inuya-Mapuya localities revealed serrated ziphodont teeth identical in size and shape to those of *S. huilensis* (Fig. 1 B; Langston, 1965: Pl. 1A) confirming its presence in the area.

Gavialid material is confined to the genus *Gryposuchus*. A partial mandible of an adult (MUSM 650; Fig. 1C) bears a long symphysis reaching posteriorly to the level of the nineteenth tooth. The tip of the dentary is heart-shaped with the first alveolus being the largest in the mandible. The splenial extends forward to the level of the twelfth tooth. Parallel lateral margins are bluntly serrated. Described characters correspond with *G. colombianus* from La Venta (Langston and Gasparini, 1997). However, MUSM 650 shows all the interalveolar spaces longer than the adjacent alveoli and, as a consequense, a proportionally longer rostrum than *G. colombianus* in which the interalveoli-alveoli space is equal. A partial symphysis (MUSM 609) about half the size of the former might belong to the same taxon. Expectable differences beetwen both specimens due to ontogenetic age are noticed (see Langston and Gasparini, 1997), though in MUSM 609 the presence of the anterior tip of the splenial reaching the level of the fourteenth alveolus is striking.

Alligatoroidea are definitely the most diverse group of crocodiles in the Peruvian Fitzcarrald Arch, but still scarcely understood. In 1961, Matthiessen detailed his discovery of a "giant mandíbula", in fact a snout of the enormous *Purussaurus*, in Quebrada Grasa (Grease Creek) of the Río Mapuya. Matthiessen's specimen (MRU 17; Fig. 1 D) possesses five premaxillary alveoli and ten maxillary alveoli, being the tenth of either of the maxilla broken in its anteriormost area. The third and fourth premaxillary alveoli are the largest in this specimen. The rostrum is short relative to its width as in *P. brasiliensis*. It ends in a bluntly rounded snout remarkably deeper than its proximal region. External naris is greatly enlarged as is typical in species of *Purussaurus*. During Fitzcarrald Expeditions, the authors found additional material of *Purussaurus*, including a complete left femur (MUSM 992; Fig. 1 I) from Alto Urubamba locality. The femur is long, robust, and sigmoidal in dorsal view. The femoral head is expanded. The fourth trochanter is a prominent crest-like structure. Total length of the femur is ~54.5 cm, representing by now the largest documented femur of a crocodile. Using femur length, an estimated total body length of this extinct crocodile is about 7.79 m (pers. com., Farlow, 2007). A quick skull-based total length estimates of Matthiessen's specimen and *P. brasiliensis* (UFAC 1403) using the scatter plot and regression of Sereno *et al.* (2001) is about 10.50–11.00 m. In general, predictions based on femoral dimensions of large crocodiles are shown

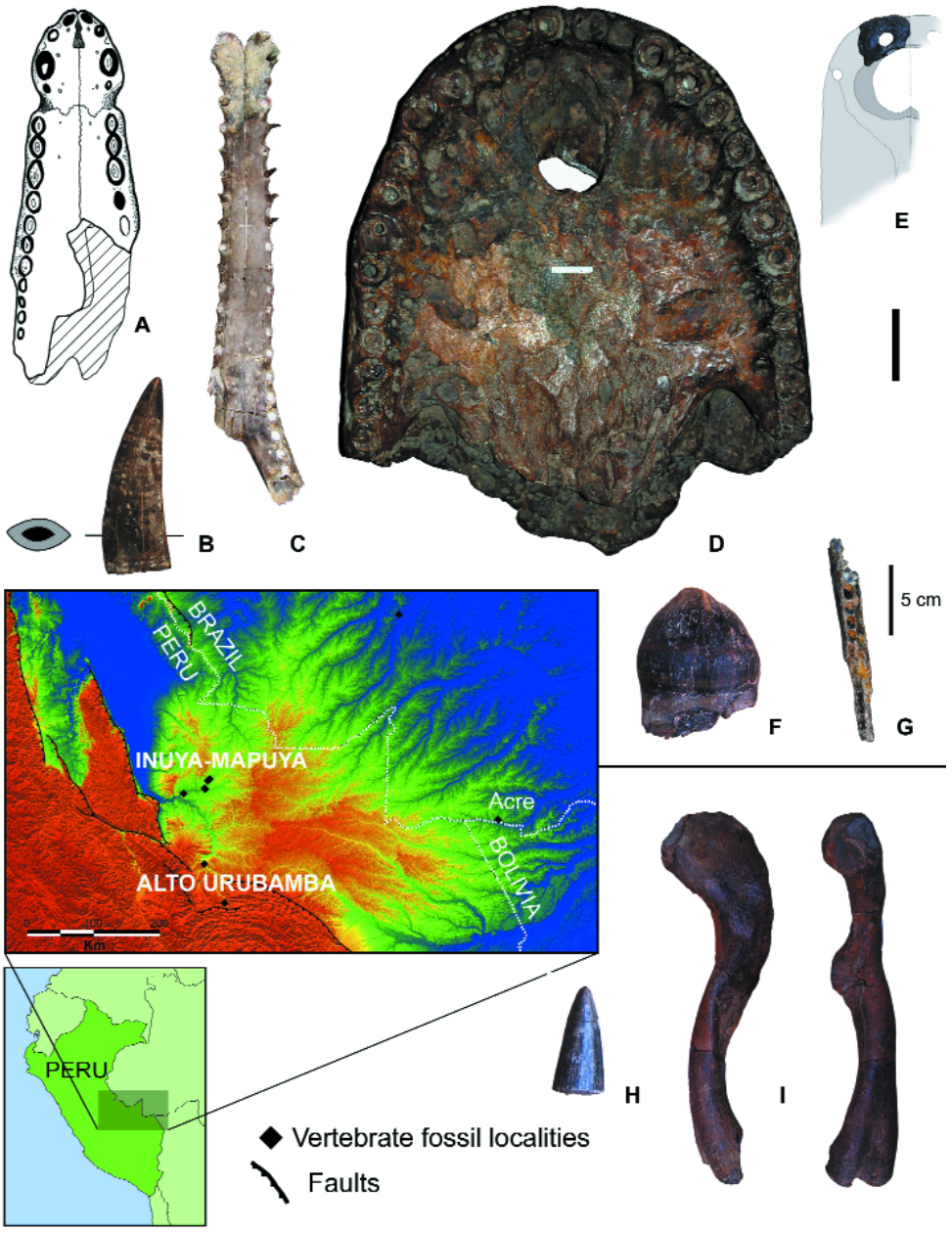

Figure 1. Map of the Fitzcarrald Arch and fossil crocodiles from the Inuya-Mapuya (A-G) and Alto Urubamba (H-I) localities, Peru. A. Sebecidae indet.: snout in occlusal view (after Buffetaut and Hoffstetter, 1977); B. *Sebecus huilensis*: MUSM 912, tooth in lateral view and cross section; C. *Gryposuchus* cf. *colombianus*: MUSM 650, partial jaw in occlusal view; D, I. *Purussaurus* sp.: D. MRU 17, snout in occlusal view and; I. MUSM 992; left femur in dorsal and medial view; E. *Mourasuchus* sp.: MUSM 931, left partial premaxilla and outline of the surrounding bones in dorsal view; F. *Balanerodus logimus*: MUSM 1261, tooth in anterior view; G. *Paleosuchus* sp.: MUSM 929, right partial dentary in occlusal view; H. aff. *Caiman* sp.: MUSM 1264, tooth in lateral view. Scale bar for all bones equals 10 cm except for G (5 cm) and teeth (actual size).

to be smaller than estimates based on other osteological data (e.g., skull), owing to the reduction of the femur relative to the body size (Farlow, 2005). As suggested by Farlow, this condition can be related with a more aquatic lifestyle. *Purussaurus* material from the Peruvian Fitzcarrald area is currently under study.

Eccentric duck-faced nettosuchids are recorded for the first time in Peru. Quarrying in a bone bed at the Mapuya River bank, a partial premaxilla (MUSM 931; Fig. 1 E) and a portion of a dentary (MUSM 930) of equivalent size belonging to the genus *Mourasuchus* were found. In both, preserved alveoli (?2-3) are comparatively bigger than in *M. atopus* from La Venta and similar to *M. nativus* from Acre. The premaxilla is robust, deep and a huge rounded pit, for the first mandibular tooth, perforates the roof lateral to a sharp narial rim. An isolated tooth of the enigmatic *Balanerodus logimus* was unearthed in a bone bed at the Inuya River (Fig. 1 F). This alligatorid was originally recognized in La Venta by teeth of peculiar subspherical shape with radiating crenulations and a coronal coarse ridge (Langston, 1965; Langston and Gasparini, 1997).

Modern genera of crocodiles are also present in these Neogene deposits. We discovered two partial dentary of the smooth-fronted caiman *Paleosuchus* (Fig. 1 G) and several teeth to species of *Caiman* affinities (Fig. 1 H). The dentary of *Paleosuchus* (MUSM 929) preserves six laterally compressed alveoli, from the twelfth to the seventeenth alveolus. Lateral to them, four occlusal pits for the maxillary teeth are much deeper than in modern specimens of this genus.

CONCLUSIONS

The new Fitzcarrald fauna of Neogene crocodiles from tropical South America represents an interesting model of great biodiversity. Our actual record of eight species, shows an assemblage of distantly-related taxa and most—if not all—morphotypes in crocodiles snouts (*sensu* Brochu, 2001). Crocodiles from Fitzcarrald include the non-eusuchian oreinirostral Sebecidae, the longirostrine Gavialidae, duck-faced Nettosuchidae, and blunt-snouted and generalized Alligatoridae. Such disparate morphologies imply ecological segregation, therefore multiple habitat ecosystems and abundance/variety of available resources. Among Sebecidae, the medium-sized *Sebecus huilensis* and the huge-sized indeterminated species were predators of different trophic level and probably of terrestrial habits (e.g., Langston, 1965). Within eusuchians, one of the largest species of all the times inhabited this territory. The generalized 'duck-faced' *Purussaurus*, with a total body length estimates of about 7.79–11.00 m, was the biggest crocodile during Tertiary times. Its presence in Negeone deposits suggest the existence of a vast aquatic ecosystem longitudinally connected in tropical South America, including actual *Purussaurus* localities in Venezuela, Colombia, Perú, Bolivia, and western Brazil. Proposed diets for some Fitzcarrald species are piscivorous (*Gryposuchus*), durophagous (*Balanerodus logimus*), filtering feeding (*Mourasuchus*), among others (Langston, 1965). It seems to be that 'diet and habitat partitioning' is the norm for sympatric crocodilian species. This condition has been observed in the four modern caiman species—with no significant differences in snout morphotypes—that occur in aquatic environments of the central Amazonian basin (Farlow and Pianka, 2002). The marine-like megalake Pebas complex, identified in the Neogene Fitzcarrald deposits (Espurt, *et al.*, 2006), constitutes the long-lasting ecosystem that provided favorable conditions for the adaptative radiation of crocodiles in tropical South America. Similar environments were proposed for La Venta (Kay and Madden, 1997), Acre (Cozzuol, 2006), and Urumaco (Sánchez-Villagra and Aguilera, 2006).

If characteristics of actual data is not an artifact of the fossil record, Fitzcarrald crocodile fauna resembles more the Middle Miocene La Venta fauna than any other fauna, sharing at least three rare species.

Sebecus huilensis and *Balanerodus logimus* are only described for La Venta and Fitzcarrald so far. Gavialidae are far from being diverse in both localities: the single *Gryposuchus* species discovered in Fitzcarrald is closely related to *G. colombianus*, the only gavialid species from La Venta (Langston and Gasparini, 1997). This taxon is not mentioned among the four and five gavialids listed for Acre and Urumaco, respectively (Cozzuol, 2006; Sánchez-Villagra and Aguilera, 2006). On the other hand, Fitzcarrald and Acre seems to share similar taxa, such as the wide-ranged nettosuchid *Mourasuchus* and alligatorid *Purussaurus*. At this point, Fitzacarrald and Urumaco crocodiles assemblages are completely distinct at species level. Based on crocodile assemblage from Fitzcarrald area, a late Middle Miocene age is assumed. It supports previous estimations given by the vertebrate fauna as a whole (Salas-Gismondi, 2006; Antoine *et al*., this volume).

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REFERENCES

Antoine, P.-O., Baby, P., Benammi, M., Brusset, S., De Franceschi, D., Espurt, N., Goillot, C., Pujos, F., Salas-Gismondi, R., Tejada, J., and Urbina M., this volume. The Middle Miocene (Laventan) Fitzcarrald fauna, Amazonian Peru.

Brochu, C. (2001). Crocodylian snouts in space and time: Phylogenetic approaches toward adaptative radiation. Amer. Zool., 41: 564-585.

Buffetaut, E. and Hoffstetter R. (1977). Découverte du Crocodilien *Sebecus* dans le Miocène du Pérou oriental. C. R. Acad. Sc. Paris, 284 (Série D): 1663-1666.

Busbey, A. (1986). New material of *Sebecus* cf. *huilensis* (Crocodylia: Sebecosuchidae) from the Miocene of La Venta Formation of Colombia. J. Vert. Paleont., 61: 20-27.

Cozzuol, M. (2006). The Acre vertebrate fauna: Age, diversity, and geography. J. South Amer. Earth. Sci., 21:185-203.

Espurt, N. , Baby, P., Brusset, S., Antoine, P.-O., Salas-Gismondi, R., Pujos, F., Roddaz, M., Regard, V., Tejada, E., and Bolaños, R. (2006). Geomorphic and sedimentologic analyses on the Fitzcarrald Arch: Evidence of a recent tectonic uplift. *XIII Congreso Peruano de Geología*, Lima, Perú, 273-276.

Espurt N., Baby P., Brusset S., Roddaz M., Hermoza W., Regard V., Antoine P.O., Salas-Gismondi R., and Bolaños R. (2007). Influence Control of the Nazca Ridge subduction on the modern Amazonian retro-foreland basin. Geology, 35: 515-518.

Farlow, J. and Pianka, E. (2002). Body size overlap, habitat partitioning and living space requirements of terrestrial vertebrate predators: implications for the paleoecology of large theropod dinosaurs. Historical Biology, 16: 21-40.

Farlow, J., Hurlburt, G., Elsey, R., Britton, A., and Langston, W. (2005). Femoral dimensions and body size of *Alligator mississippiensis*: estimating the size of extinct mesoeucrocodylians. J. Vert. Paleont., 25: 354-369.

Kay, R., and Madden, R. (1997). Paleogeography and paleoecology. pp. 520-550 in: Kay R., Madden R., Cifelli R., and Flynn, J. (Eds.). Vertebrate Paleontology in the Neotropics. The Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington and London.

Langston, W. (1965). Fossil crocodilians from Colombia and the Cenozoic History of the Crocodylia in South America. University of California Publications of Geological Sciences, 52: 1-127.

Langston, W. and Gasparini Z. (1997). Crocodilians, *Gryposuchus*, and the South American Gavials; pp. 113-154 in: Kay R., Madden R., Cifelli R., and Flynn, J. (Eds.). Vertebrate Paleontology in the Neotropics. The Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington and London.

Matthiessen, P. (1961). The Cloud Forest. Ballantine Walden Editon, 287 pp.

Salas, R. and Urbina, M. (2003). El especimen de *Purussaurus* (Eusuchia: Alligatoridae) del Mioceno superior del Río Mapuya, Ucayali-Perú. VI Congreso Latinoamericano de Herpetología, Lima-Perú: 95R.

Salas-Gismondi, R., Baby, P., Antoine, P.-O., Pujos, F., Benammi, M., Espurt, N., Brusset, S., Urbina, M., and De Franceschi, D. (2006). Late middle Miocene vertebrates from the Peruvian Amazonian Basin (Inuya and Mapuya Rivers, Ucayali): Fitzcarrald Expedition 2005. *XIII Congreso Peruano de Geología*, Lima, Perú, 643-646.

Sánchez-Villagra, M. and Aguilera, O. (2006). Neogene Vertebrates from Urumaco, Falcon State, Venezuela: diversity and significance. J. System. Palaeont., 4: 213-220.

Sereno, P. (2001). The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. Science, 294:1516-1519.

Wesselingh, F., Räsänen, M., Irion, G., Vonhof, H., Kaandorp, R., Renema, W., Romero-Pittman, L., and Gingras, M. (2002). Lake Pebas: palaeoecological reconstruction of a Miocene, long-lived lake complex in western Amazonia. Cain. Res., 1(1-2): 35-81.