First post-Mesozoic record of Crocodyliformes from Chile

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Fossil crocodilians are well known from vertebrate bearing localities in South America, but the last record of the group in Chile is from the Cretaceous. No living crocodilians occur in Chile today, and the timing of their disappearance from the country is unknown. We provide the first post-Mesozoic report of crocodilian remains from late Miocene marine deposits of the Bahía Inglesa Formation, northern Chile. The fragmentary material provides proof that Crocodiliformes were present in Chile until at least seven million years ago. We suggest that late Neogene climatic cooling and changes in South American palaeophysiography caused the extinction of the group in Chile.

Key words: Crocodyliformes, climate change, extinction, Bahía Inglesa Formation, Neogene, Chile.

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Introduction

Crocodilians have a long and diverse fossil record in South America, with Tertiary freshwater and terrestrial deposits in particular having provided exceptionally rich faunas. In fact, crocodilians are encountered throughout much of the South American Tertiary, and are known from Argentina, Brazil, Colombia, Peru, and Venezuela (Langstone 1965; Buffetaut 1982; Gasparini 1996; Brochu 1999; Kay et al. 1997; Lopez 1997). South American crocodilians are rarer in Tertiary marine sequences, the only reports coming from the early Miocene of Venezuela (Sánchez-Villagra et al. 2001; Brochu and Rincon 2004) and Mio-Pliocene of Peru (Muizon and DeVries 1985; Kraus 1998).

South America also has one of the most diverse living crocodilian faunas of any continent, with eight of the 23 extant species present, six of which are caimans. Chile is the only South American country lacking crocodilians, although they do occur in adjacent countries. Fossil crocodilians from Chile are mainly marine forms from the Jurassic of northernmost Chile (e.g., Chong and Gasparini 1972; Gasparini and Dias 1977; Gasparini 1980). Fragmentary remains of only one continental form are known from Cretaceous sediments of central-northern Chile (Suárez et al. 2002) and represent the latest occurrence of the group in that country. Assuming the presence of suitable habitats, crocodilians are likely to have been present in Chile during the Cenozoic, yet none has been reported from Chilean Tertiary sequences. This regional lack of fossils represents a barrier to our understanding of the former distribution and diversity of the group.

We present here the first post-Mesozoic record of crocodilians in Chile, based on a right dentary fragment, proximal portion of a right tibia and an isolated tooth from the Bahía Inglesa Formation of northern Chile. The occurrence of these specimens in late Miocene sediments demonstrates that crocodilians were present in Chile until at least seven million years ago.

Institutional abbreviations.—BMNH, Natural History Museum, London, United Kingdom; MNHN, Muséum National d'Histoire Naturelle, Paris, France; SGO-PV, Sección Paleontología, Museo Nacional de Historia Natural, Santiago, Chile; SMNK, Staatliches Museum für Naturkunde, Karlsruhe, Germany.

Geology and age of the Bahía Inglesa Formation

The marine Bahía Inglesa Formation (Fig. 1B) consists of over 42 m of siltstones, fine sands, shelly coquinas, pebble beds, and phosphatites, and represents a shallow marine setting deposited within 10 km of the shore (Marquardt et al. 2000; Walsh 2002). An important exposure of the Bahía Inglesa Formation occurs in an area of arid badlands 1 km inland of Bahía Inglesa bay, on the coast of north-central Chile (S27°06´ 43·5´´ W70°50´ 09·8´´ and S27°09´ 58·6´´ W70° 52´ 32·4´´ (Fig. 1A). The closest settlement is the village of Bahía Inglesa, and the nearest town is Caldera, some 5 km and 10 km northeast of the study area respectively. In this area the sequence was deposited in a series of grabens formed in the Mesozoic igneous basement (Godoy et al. 2003), today visible as a series of roughly NE-SW trending inliers.

Three lithostratigraphic members are recognisable in this region; the coarse conglomeratic basal Morro Member (Unit 1

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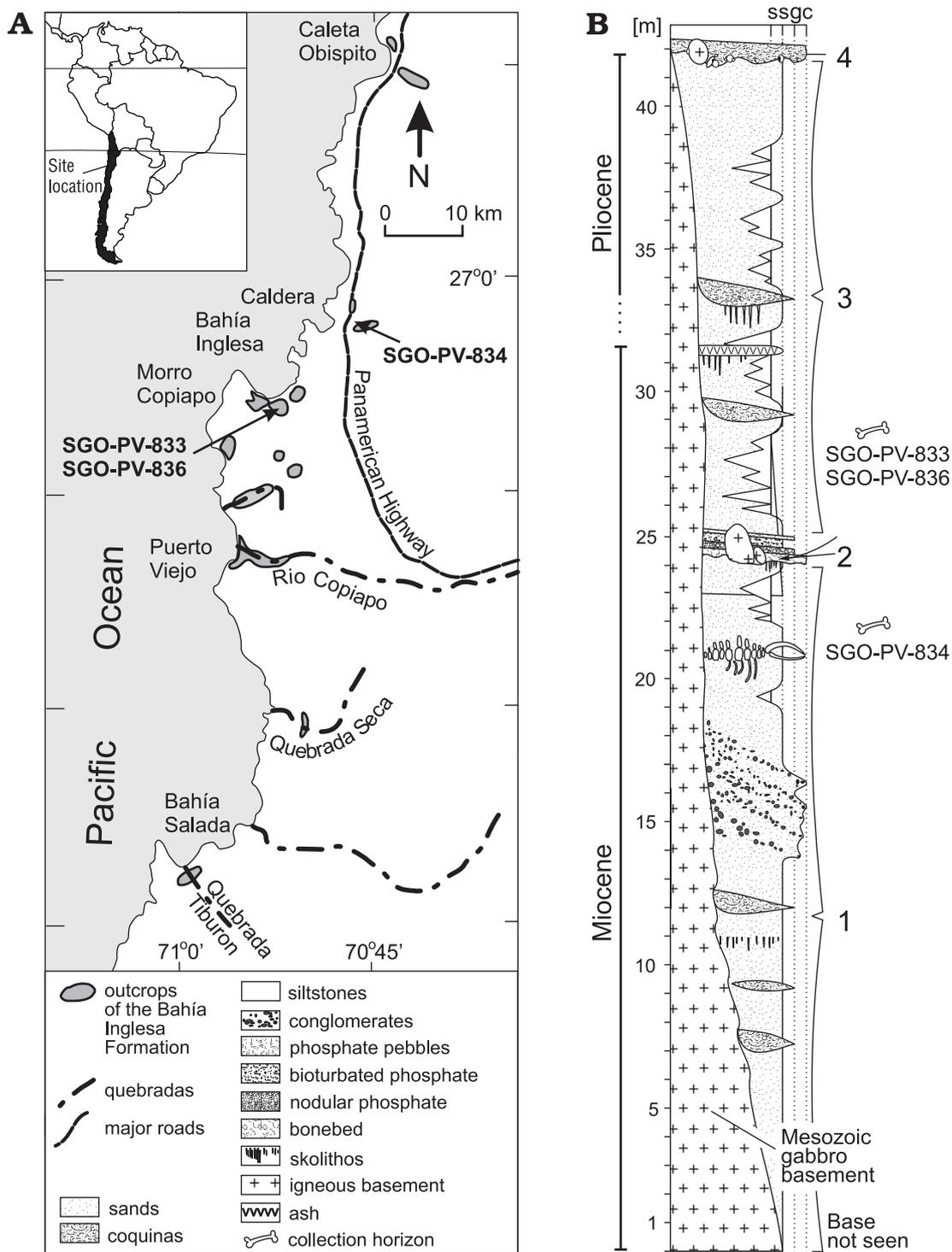
Fig. 1. **A**. Site location. **B**. Generalised stratigraphic log of the Bahía Inglesa Formation. 1, Morro Member. Medium/coarse sands with *Skolithos* and crossbedding. Sands intercalated with coquinas, grading into pale fish-bearing siltstones to the north-east. Conglomerates present at some levels; 2, Bahía Inglesa Formation Bonebed Member. Phosphorites intercalated with fine/medium sands. The Bahía Inglesa Formation Bonebed marks the base; 3, Lechero Member. As Bahía Inglesa Formation Bonebed Member, but without phosphorites; 4, Early Pleistocene marine terrace downcuts toward bay. ssgc, sedimentary clast size division: silt, sand, gravel, and cobbles.

of Walsh and Hume 2001); the phosphoritic Bahía Inglesa Formation Bonebed Member (Unit 2 of Walsh and Hume 2001), and the fine sand and siltstone Lechero Member (Unit 3 of Walsh and Hume 2001). A phosphatite (*sensu* Slansky 1986) bonebed with a lateral extent of around four km² occurs at the base of the Bahía Inglesa Formation Bonebed Member. This horizon comprises up to 77% (mostly fragmentary) vertebrate remains that, in addition to crocodilian fossils, include
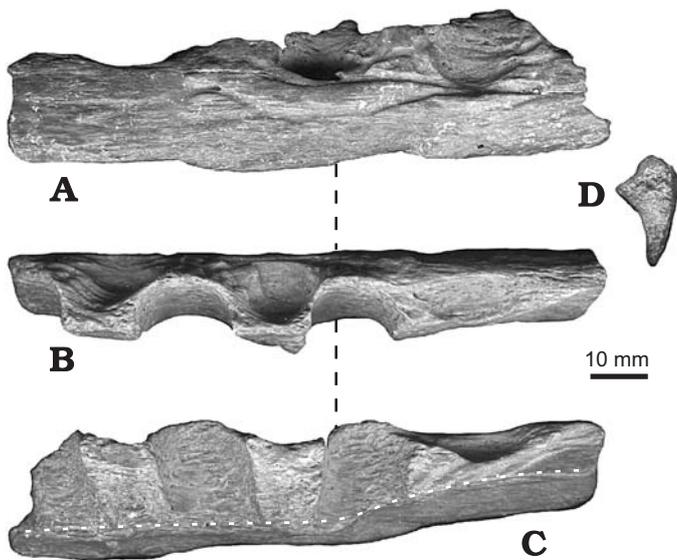
Fig. 2. Indeterminate crocodilian right dentary fragment (SGO-PV 834, Bahía Inglesa, Chile, late Miocene) in lateral (**A**), occlusal (**B**), medial (**C**), and caudal (**D**) aspects. Dashed line in white (in C) indicates position of Meckel's groove.
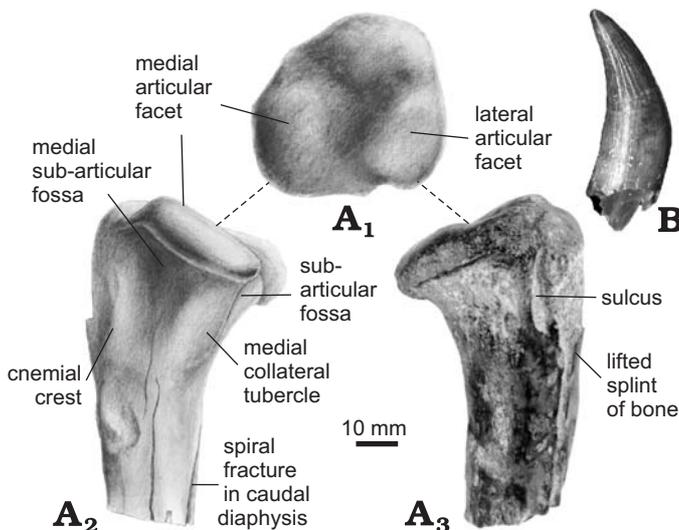
Fig. 3. **A**. Indeterminate crocodilian right tibia (SGO-PV-833, Bahía Inglesa, Chile, late Miocene) in proximal (A_1), medial (A_2), and lateral (A_3) aspects. Note the spiral fractures in A_2 and A_3. Such fractures involve torsional stress and indicate that the bone was fresh when the fracture occurred (see Lyman 1994 for a review of spiral fracture aetiology). Since impact during wave action or burial compaction seem unlikely to have caused the fracture, it may be direct evidence for predation or scavenging by other crocodyliforms. **B**. Indeterminate crocodilian tooth (SGO-PV-836, Bahía Inglesa, Chile, late Miocene). A_1 and A_2 are pencil drawings, A_3 and B are photographs.

sharks, rays, bony fish, seabirds, sloths, seals, whales and dolphins (Walsh 1999, 2003; Walsh and Hume 2001; Walsh and Naish 2002; Suárez and Marquardt 2003; Suárez et al. 2004). A right crocodilian tibia fragment (SGO-PV-833) and tooth (SGO-PV 836) were recovered from this horizon. A right crocodilian dentary fragment (SGO-PV-834) was collected

from the Arenas de Caldera (Morro Member), south-east of Caldera (Fig. 1A).

The age of the Bahía Inglesa Formation bonebed can be constrained using radiometric data, and microfossil and vertebrate assemblages in the beds above and below. Based on microfossil biostratigraphy the overlying Lechero Member is 4.5–2.6 Ma (Tsuchi et al. 1988; Ibaraki 1995). The shark assemblage of this member is characterised by the abundance of *Carcharodon carcharias* (Long 1993), and the additional presence of *Prionace glauca* provides good evidence supporting a Pliocene age (Suárez and Marquardt 2003). However, an ash layer occurs within the Lechero Member, approximately seven metres above the top of the Bahía Inglesa Formation Bonebed Member. This provides a K-Ar age of 7.6 ± 1.3 Ma (Marquardt et al. 2000; Godoy et al. 2003), indicating that the lower part of the Lechero Member is late Miocene, and thus the bonebed is no younger than Tortonian. Although the shark fauna of the bonebed is dominated by *Cosmopolitodus hastalis*, *Carcharodon carcharias* is present in low abundances. The teeth of these species have been used to differentiate Miocene from Pliocene sediments in South America (e.g., Muizon and DeVries 1985; Walsh and Hume 2001; Walsh and Naish 2002), but the presence of *C. carcharias* in Chilean beds well dated as Miocene suggests that their use should be accompanied by caution. The presence of the monachine seal *Acrophoca* sp. below the bonebed at the top of the Morro Member (Walsh and Naish 2002) indicates that these beds are unlikely to be older than middle Miocene, as this is the age of the first recognisable monachine (Muizon 1982). However, as the first occurrence of *Acrophoca* sp. (Muizon and DeVries 1985) in Peru is late Miocene, the top of the Morro Member is probably no older than late Miocene.

We therefore propose a late Miocene (Tortonian) age for SGO-PV-833 and SGO-PV 836 (Fig. 1B). Based on its chondrichthyan fauna (with an abundance of *Cosmopolitodus hastalis* and absence of *C. carcharias*) Suárez et al. (2004) assigned a mid- to late Miocene age to the Arenas de Caldera level from which SGO-PV-834 was recovered (Fig. 1B).

Systematic palaeontology

Crocodylomorpha Walker, 1970
Crocodyliformes Benton and Clark, 1988
Crocodyliformes *incertae sedis*

Material.—Right dentary fragment (SGO-PV-834), right tibia (SGO-PV-833), isolated tooth (SGO-PV 836).

Description

Dentary fragment (Fig. 2A–D).—This element comprises a fragment of right dentary 150 mm long and 25 mm at its highest point. The caudal extremity of the specimen represents a post-fossilisation breakage, and there is no evidence of contact with the splenial. In medial view (Fig. 2C)

Meckel's groove is very thin rostrally, becoming higher and broader by the level of the caudalmost alveolus, suggesting that the fragment represents a more rostral region of the ramus. The lateral surface of the specimen (Fig. 2A) is strongly ornamented, and bears two foramina close to the rostral fracture line. Two alveoli and part of a third are preserved (average diameter 15 mm). Three occlusal pits for the corresponding upper teeth are also present, indicating that the upper and lower dentition interlocked (Fig. 2A, B). The two rostralmost alveoli are round, while the caudal alveolus is more ovoid. The diastemata average 12 mm in width. In lateral view the dorsal margin is approximately straight, widening locally around the alveoli.

Proximal tibia (Fig. 3A$_1$, A$_2$, A$_3$).—The proximal condyles and part of the diaphysis are preserved in this fragment. With a length of 79 mm and a maximum craniocaudal width of 47 mm, it is comparable in size with specimens *Crocodylus niloticus* held by the BMNH, suggesting that the Bahía Inglesa fossil taxon was similar in size to this extant species. The diaphysis is curved caudally in lateral view (Fig. 3A$_3$), and straight in cranial view. The proximal epiphysis is strongly expanded caudally and mediolaterally with a medially inclined articular surface bearing slightly convex lateral and medial articular facets (Fig. 3A$_1$). The cnemial crest is poorly developed but confluent with the long axis of the diaphysis, widening proximally and extending to the distal fracture line. Well-defined medial and lateral collateral tuberculae are situated caudally on their respective surfaces. A narrow and deep sulcus is present below the articular surface on the lateralmost margin of the cranial surface (Fig. 3A$_3$).

Tooth (Fig. 3B).—This specimen is 55 mm long, and lacks only the basalmost portion of the root. The crown is 24 mm high, bears well-developed, regularly spaced longitudinal folds that are not appreciably worn, and lacks carinae. At 15 mm in diameter the root is consistent with the size of the alveoli in SGO-PV-834.

Discussion

This material represents the first record of reptiles in the Bahía Inglesa Formation and also from Tertiary marine deposits of Chile. The possibility exists that the specimens are referable to more than one taxon, but as this cannot presently be determined we provisionally regard these specimens as representing a single taxon. Comparison of the material with osteological specimens of extant crocodilians held at BMNH, MNHN, and SMNK indicates that the Bahía Inglesa crocodilian is not referable to any living species.

Identification of these specimens beyond the level of Crocodyliformes has proved problematic due to their fragmentary nature, and it is presently unclear even to what extent this taxon is a "marine" form. Attempting to determine the osmoregulatory capability of extinct crocodilians from fossil evidence is problematic, and may in any case be a poor guide to their actual behaviour. For instance, despite their supposedly poor saltwater adaptations, alligatorids sometimes are encountered in saltwater, and certainly can disperse across relatively narrow marine barriers (Brochu 1999; Moulton et al. 1999). However, although the Bahía Inglesa specimens could have been transported from inland by fluvial processes they are not appreciably abraded, and the rarity of terrestrial taxa in the Bahía Inglesa Formation suggests that fluvial transport of vertebrate remains into the marine environment was minimal (Walsh 2002). Based on the environment of deposition, the Bahía Inglesa crocodilian appears to have been an inhabitant of shallow coastal areas, although this does not preclude the possibility that these specimens represent the remains of infrequent visitors to the region.

Gharials, caimans, and the extinct sebecosuchians were present in South America during the Neogene (e.g., Langston and Gasparini 1997; Sánchez-Villagra et al. 2001; Brochu and Rincon 2004), and it is likely that our material is referable to one of these rather than to a crocodyline. Unfortunately, it is not possible to assign this material to any of these groups, as none of these specimens possesses characters that would allow confident referral to a specific crocodyliform clade. However, the lack of serrations in the tooth SGO-PV-836 indicates that it does not belong to a sebecosuchian. The marine context of deposition also makes referral of any of these specimens to the Sebecosuchidae unlikely, as this family appears to have been primarily terrestrial (Gasparini 1984). Alligatorids normally possess narrower lower jaws that allow the upper teeth to occlude outside the lower teeth. Since the teeth of SGO-PV-834 clearly interlocked with well-defined occlusal pits, the Bahía Inglesa crocodilian is unlikely to be referable to an alligatorid.

The dorsal margin of the dentary in extant brevirostrine crocodylines and alligatorids is straight between the two dentary peaks, but only in longirostrine forms such as *Gavialis* and *Tomistoma* is the dorsal margin straight along its entire length. Although incomplete, the approximately straight dorsal margin of SGO-PV-834 certainly suggests that it may have belonged to a similar longirostrine form. The Bahía Inglesa crocodilian could be a tomistomine, but as only gharials are the only crocodilians known with certainty from Neogene marine sequences of the western and northern coasts of South America (e.g., Muizon and DeVries 1985; Kraus 1998; Sánchez-Villagra et al. 2001; Brochu and Rincon 2004) it would seem more likely that it belongs to this group. The fossil gharial *Piscogavialis jugaliperforatus* (Kraus 1998) is known from the Pisco Formation of Peru some 1600 km north of Bahía Inglesa. However, despite a strong faunal similarity between the Pisco and Bahía Inglesa formations (Walsh and Hume 2001; Walsh and Naish 2002), comparison of this material with the holotype of *P. jugaliperforatus* (SMNK 1282 PAL) indicates that the Chilean and Peruvian taxa are not conspecific. Firstly, whilst SGO-PV-834 is similar in morphology and tooth pattern to the corre-

sponding region of the dentary in *P. jugaliperforatus*, the dentary in that species lacks the pronounced occlusal pits seen in the Bahía Inglesa specimen. Furthermore, the tibia of *P. jugaliperforatus* is less craniocaudally curved, with a shallower angled articular surface than seen in SGO-PV-833. Consequently, although the Bahía Inglesa crocodilian may be a gharial or a tomistomine we await discovery of more diagnostic material to verify this.

The occurrence of crocodilian remains in the Bahía Inglesa Formation demonstrates that crocodilians were present in Chile during the late Miocene, and possibly also during the Pliocene. The absence of crocodilian species in Chile today must therefore be due to a post-late Miocene extinction event. In the Peruvian Pisco Formation gharial remains are last observed in the late Pliocene (Muizon and DeVries 1985). There is some evidence that Chile belonged to a warm-temperate province at that time (Martínez and Martínez 1997), and it is probable that crocodilians also continued to be present in the Bahía Inglesa region.

The causes of their extinction remain unclear, but it seems very likely that climatic cooling toward the end of the Neogene played a major role. The aridity that has affected northern Chile since at least the mid-Miocene (e.g., Flower and Kennett 1994; Hinojosa and Villagran 1997) would have compounded the reduction of fluvial discharge caused when the Andean Coastal Range reached its present elevation in the Pliocene (e.g., Rogers 1993). Any crocodilian populations inhabiting rivers and estuaries would have been strongly affected as the river systems of northern Chile shrank. Thus, climatic cooling and loss of habitat may have acted to decimate breeding populations of any riverine crocodilians, resulting in their eventual extinction in the region. This unfavourable environment remains a feature of the region today, and it seems unlikely that populations of riverine crocodilians could be sustained even if they had later been able to cross the physical barrier of the Andean Range to recolonise the area.

With a range from at least northern Chile to Venezuela, marine gharials were apparently widespread along the South American coast. Assuming they were less dependent on the presence of suitable rivers and estuaries, their disappearance by the end of the Neogene is unlikely to be related to river system shrinkage. One possibility is that Pliocene cooling of the coastal currents (e.g., Ibaraki 2001) made crocodilian populations unviable off Chile and Peru. However, uplift of the Panamanian Isthmus has been suggested to have initially driven a period of climatic warming between 4.7 and 3.1 Ma (Billups et al. 1999; Haug et al. 2001). Unless the extinction occurred after this time, this period of warming is inconsistent with an extinction mechanism related to thermal deterioration. This scenario also does not explain the extinction of the Venezuelan gharials, which would have continued to inhabit warmer waters (e.g., Billups et al. 1999). Alternatively, it is possible that changes in oceanic circulation resulting from closure of the Panamanian Seaway led to a crash in populations of whatever prey the gharials relied on. Correlation

of the last occurrence of the group in each area with known eastern Pacific oceanographic events would be required to test these hypotheses. Although our record provides new evidence that may in future make such a study possible, the exact cause of the disappearance of the South American marine gharials must for now remain a mystery.

Acknowledgements

References

Benton, M.J. and Clark J.M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. *In*: M.J. Benton (ed.), The Phylogeny and Classification of the Tetrapods. Volume 1: Amphibians, Reptiles and Birds. *Systematics Association Special Volume* 35A: 295–338.

Billups, K., Ravelo, A.C., Zachos, J.C., and Norris, R.D. 1999. Link between oceanic heat transport, thermohaline circulation, and the Intertropical Convergence Zone in the early Pliocene Atlantic. *Geology* 27: 319–322.

Brochu, C.A. 1999. Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. *Journal of Vertebrate Paleontology* 11 (Supplement to No. 4), Memoir 6: 9–100.

Brochu, C.A. and Rincon, A.D. 2004. A gavialoid crocodylian from the Lower Miocene of Venezuela. *In*: M.R. Sánchez-Villagra and J.A. Clack (eds.), Fossils of the Miocene Castillo Formation, Venezuela: Contributions on Neotropical Palaeontology. *Special Papers in Palaeontology* 71: 61–80.

Buffetaut, E. 1982. Systématique, origine et évolution des Gavialidae Sud-Americans. *Geobios, Mémoire spécial* 6: 127–140.

Chong, G. and Gasparini, Z.B. 1972. Presencia de Crocodilia marinos en el Jurásico de Chile. *Revista de la Asociación Geologico de Argentina* 24: 406–409.

Flower, B.P. and J.P. Kennett. 1994. The middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108: 537–555.

Gasparini, Z. and Díaz, G.C. 1977. *Metriorhynchus casamiquelai* n. sp. (Crocodilia, Thalattosuchia), a marine crocodile from the Jurassic (Callovian) of Chile, South America. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 153: 341–360.

Gasparini, Z. 1980. Un nuevo cocodrilo marino (Crocodylia, Metriorhynchidae) del Caloviano del norte de Chile. *Ameghiniana* 17: 97–103.

Gasparini, Z. 1984. New Tertiary Sebosuchia (Crocodylia: Mesosuchia) from Argentina. *Journal of Vertebrate Paleontology* 4: 85–95.

Gasparini, Z. 1996. Biogeographic evolution of the South American crocodyliforms. *Münchner geowissenschaftliche Abhandlungen A* 30: 159–184.

Godoy, E., Marquardt, C., and Blanco, N. 2003. *Geología de la Carta Caldera, Región de Atacama. Carta Geológica de Chile. Serie Geología Básica 1, mapa escala 1:100.000*. Servicio Nacional de Geología y Minería, Santiago.

Haug, G.H., Tiedemann, R., Zahn, R., and Ravelo, A.C. 2001. Role of Panama uplift on oceanic freshwater balance. *Geology* 29: 207–210.

Hinojosa, L.F. and Villagran, C. 1997. Historia de los bosques del sur de Sudamérica, I: Antecedents paleobotánicos, geológicos y climáticos del Terciario del cono sur de América. *Revista Chilena de Historia Natural* 70: 225–239.

Ibaraki, M. 1995. Neogene chronostratigraphy of biosiliceous sediments on the Pacific coast of South America based on planctonic foraminifera. *Reports of the Faculty of Science, Shizuoka University* 29: 63–71.

Ibaraki, M. 2001. Neogene planktonic foraminifera of the Caleta Herradura de Mejillones section in northern Chile: Biostratigraphy and paleoceanographic implications. *Micropaleontology* 47: 257–267.

Kay, R.F., Madden, R.H., Cifelli, R.L., and Flynn J.J. 1997. *Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia*. 592 pp. Smithsonian Institution Press, Washington.

Kraus, R. 1998. The cranium of *Piscogavialis jugaliperforatus* n. gen., n. sp. (Gavialidae, Crocodylia) from the Miocene of Peru. *Paläontologische Zeitschrift* 72: 389–406.

Langston, W. 1965. Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America. *University of California Publications in Geological Sciences* 52: 1–157.

Langston, W. and Gasparini Z. 1997. Crocodilians, *Gryposuchus*, and the South American gavials. *In*: R.F. Kay, R.H. Madden, R.L. Cifelli, and J.J. Flynn (eds.), *Vertebrate Paleontology in the Neotropics: the Miocene Fauna of La Venta, Colombia*, 113–154. Smithsonian Institution Press, Washington.

Long, D.J. 1993. Late Miocene and Early Pliocene fish assemblages from the north central coast of Chile. *Tertiary Research* 14: 117–126.

Lopez, G.M. 1997. Paleogene faunal assemblage from Antofagasta de la Sierra (Catamarca Province, Argentina). *Palaeovertebrata* 26 (1–4): 61–81.

Lyman, R.L. 1994. *Vertebrate Taphonomy. Cambridge Manuals in Archaeology*. 524 pp. Cambridge University Press, Cambridge.

Marquardt, C., Blanco, N., Lavenu, A., Godoy, L., Ortlieb, L. Marchant, M., and Guzmán, N. 2000. Estratigrafía del Cenozoico Superior en el área de Caldera (26°45′–28°S), III Región de Atacama, Chile. *Actas del IX Congreso Geológico Chileno* 1 (3): 504–508.

Martínez-Pardo, R. and Martínez-Guzmán, R. 1997. Neogene Southeast Pacific paleoceanography, the opening of the Drake Passage and the Humboldt Current history: the Chilean micropaleontological perspective. *VIII Congreso Geologico Chileno, Antofagasta*, 525–527.

Mercado, M. 1977. *Avance Geologico de la Hoja Caldera-region de Atacama. Escala 1:250.000. Mapa No. 1*. Talleres Gráficos del Instituto Geográfico Militar, Santiago.

Moulton, T.P., Magnusson, W.E., and Queiroz Melo, M.T. 1999. Growth of Caiman latirostris Inhabiting a Coastal Environment in Brazil. *Journal of Herpetology* 33: 479–484.

Muizon, C. de. 1982. Phocid phylogeny and dispersal. *Annals of the South African Museum* 89: 175–213.

Muizon, C. de and DeVries, T.J. 1985. Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). *Geologische Rundschau* 74: 547–563.

Rogers, J.J.W. 1993. *A History of the Earth*. 312 pp. Cambridge University Press, Cambridge.

Sánchez-Villagra, M.R., Gasparini, Z., Lozsán, R., Moody, J.M., and Uhen, M.D. 2001. New discoveries of vertebrates from a near-shore marine fauna from the Early Miocene of northwestern Venezuela. *Paläontologische Zeitschrift* 75: 227–231.

Slansky, M. 1986. *Geology of Sedimentary Phosphates*. 210 pp. North Oxford Academic Publishers, Oxford.

Suárez, M.E., Pineda, G., and Torres, T. 2002. Vertebrados continentales de los estratos de Quebrada la Totora, Cretácico Inferior y tardío de Pichasca, IV Región. *Actas del Congreso Latinoamericano de Paleontología de Vertebrados* 1: 49–50.

Suárez, M.E. and Marquardt, C. 2003. Revisión preliminar de las faunas de peces elasmobranquios del Mesozoico y Cenozoico de Chile. *Actas X Congreso Geológico Chileno, Sesión temática 3, Paleontología*. CD-ROM. Universidad de Concepción, Concepción.

Suárez, M.E., Lamilla J., and Marquardt, C. 2004. Peces Chimariformes (Chondrichytyes, Holocephali) del Neógeno de la Formación Bahía Inglesa (Región de Atacama, Chile). *Revista Geológica de Chile* 31 (1): 105–117.

Tsuchi, R., Shuto, T., Takayama, T., Fujiyoshi, A., Koizumi, I., Ibaraki, M., and Martinez, P.R. 1988. Fundamental data on Cenozoic biostratigraphy of Chile. *In*: R. Tsuchi (ed.), *Reports of Andean studies, Shizuoka University-Trans-Pacific Correlation of Cenozoic Geohistory 2*, 71–95. Kofune Printing, Shizuoka.

Walker, A.D. 1970. A revision of the Jurassic *Hallopus victor* (Marsh) with remarks of the classification of crocodiles. *Philosophical Transactions of the Royal Society of London, Series B* 257: 322–372.

Walsh, S.A. 1999. A New Mio-Pliocene bone-bed from north-central Chile. *Journal of Vertebrate Paleontology* 19 (Supplement to No. 3), Abstracts: 82A.

Walsh, S.A. 2002. Taphonomy and genesis of the Neogene Bahía Inglesa Formation bonebed, northern Chile. *Journal of Vertebrate Paleontology* 22 (Supplement to No. 3), Abstracts: 117A.

Walsh, S.A. 2003. Palaeoecology of the Neogene Bahía Inglesa Formation, Chile. *In*: P.M. Barrett (ed.), *Abstracts of the 51st Symposium of Vertebrate Palaeontology and Comparative Anatomy* 33. Oxford.

Walsh, S.A. and Hume, J.P. 2001. A new Neogene marine avian assemblage from north-central Chile. *Journal of Vertebrate Paleontology* 21: 484–491.

Walsh, S.A. and Naish, D. 2002. Fossil seals from late Neogene deposits in South America: a new pinniped (Carnivora, Mammalia) assemblage from Chile. *Palaeontology* 45: 821–842.