

Choristoderes and the freshwater assemblages of Laurasia

Coristoderos y las asociaciones de agua dulce de Laurasia

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Abstract

Choristoderes are freshwater aquatic diapsid reptiles of uncertain phylogenetic position. Although the lineage probably diverged from other diapsids in the Permo-Triassic, choristoderes apparently never reached Gondwana. Within Laurasia, however, they have been recovered from Japan, China, Mongolia, Trans-Baikal Russia, Central Asia, Western Europe, and North America, reaching extreme northern latitudes. Setting aside controversial Triassic records, their known temporal range currently extends from the Middle Jurassic (Britain, Kyrgyzstan) to the Miocene (Czech Republic). However, although small choristoderes are known to span the entirety of this period, the larger, more derived neochoristoderes are recorded only from the Early Cretaceous through to the earliest Eocene. The gavial-like neochoristodere *Champsosaurus* is the most familiar taxon, characterised by large size, a long rostrum and flared temporal fenestrae, but research over the last three decades has revealed many new genera and exposed an unexpected diversity in terms of body size (small to relatively large), neck length (long v. short) and skull morphology (longirostrine v. brevirostrine, open v. closed lower temporal fenestrae). Typically choristoderes occur as part of a mesic assemblage that includes fish, lizards, mammals, turtles, frogs, salamanders, small dinosaurs and, usually, crocodiles. At maturity, Jurassic choristoderes were generally smaller than co-occurring crocodiles and were relatively unspecialized postcranially. The Early Cretaceous of Asia saw a dramatic diversification of choristoderes, including the appearance of much larger neochoristoderes. Perhaps significantly, the relevant Asian horizons (e.g. Yixian Formation, China; Okurodani and Kuwajima formations, Japan) yield no crocodiles. In Late Cretaceous and Paleogene horizons however, across Euramerica, large gavial-like neochoristoderes came to share freshwater ecosystems with a diversity of crocodiles, the neochoristoderes apparently occupying a specialist (gavial-like) piscivorous niche as long as it was available and resources were adequate.

Keywords: Choristodera, Paleobiogeography, Fauna, Laurasia, Crocodylomorpha

Resumen

Los Coristoderos son reptiles diápsidos acuáticos con posición filogenética incierta. A pesar de que el linaje probablemente divergió del resto de diápsidos en el Permo-Triásico, los coristoderos aparentemente nunca alcanzaron Gondwana. En Laurasia, sin embargo, se han registrado restos en Japón, China, Mongolia, la región Trans-Baikal de Rusia, Asia Central, Europa occidental y Norteamérica, alcanzando latitudes septentrionales extremas. Si evitamos el registro controvertido del Triásico, su rango temporal conocido se extiende desde el Jurásico Medio (Islas Británicas, Kirguizistán), al Mioceno (República Checa). Sin embargo, a pesar de que los coristoderos pequeños se sabe que existieron a lo largo de todo este periodo, los más grandes, los neocoristoderos derivados se registran sólo desde el Cretácico temprano hasta el comienzo del Eoceno. Entre los neocoristoderos el de tipo gavial, *Champsosaurus*, es uno de los taxones más conocidos, caracterizado por su gran talla, un rostro alargado y amplias fosas temporales, sin embargo, las investigaciones desarrolladas durante las tres últimas décadas han revelado muchos géneros nuevos y puesto de manifiesto una diversidad inesperada en relación con su tamaño corporal (de pequeño a relativamente grande), la longitud del cuello (largo-corto) y la morfología del cráneo (longirostros-brevirostros; o con ventanas temporales inferiores cerradas). Habitualmente los coristoderos forman parte de asociaciones métricas que incluyen a peces, lagartos, mamíferos, tortugas, salamandras, pequeños dinosaurios, y habitualmente cocodrilos. Al alcanzar la madurez, los coristoderos jurásicos fueron generalmente más pequeños que los cocodrilos de la misma asociación, y además con pocas especializaciones postcraneales. En el Cretácico temprano de Asia se dieron las condiciones para una extraordinaria diversificación de los coristoderos, incluyendo la aparición de formas de neocoristoderos de porte mucho mayor. De modo significativo, en los importantes depósitos asiáticos como los de la Formación Yixian, China; o los de las Formaciones Okurodani and Kuwajima, Japón, los cocodrilos están muy posiblemente ausentes. En horizontes del Cretácico Superior y del Paleógeno, sin embargo, y a lo largo de Suramérica, las formas de neocoristoderos de tipo gavial compartieron ecosistemas de agua dulce con una diversidad de cocodrilos, los neocoristoderos aparentemente ocuparían un nicho piscívoro especializado (de tipo gavial) en tanto que disponían de recursos adecuados.

Palabras clave: Choristodera, Paleobiogeografía, Fauna, Laurasia, Crocodylomorpha.

1. Introduction

Choristodera was erected by Cope (1876) to encompass *Champsosaurus*, a new fresh water reptile from the Upper Cretaceous Judith River beds of Montana, North America. A year later, Gervais (1877) described *Simoedosaurus* from the Upper Paleocene at Cernay, near Reims, France. These two genera were the only representatives of Choristodera for more than a century, but over the last three decades, new discoveries have extended the temporal and geographical range of the group, and provided increased understanding of its diversity. Choristoderes have been found across Laurasia, from Japan in the east to Alberta in the west (e.g. Evans and Hecht 1993; Gao and Fox, 1998; Matsumoto *et al.*, 2007, 2009) in deposits ranging in age from Middle Jurassic to Miocene. However, despite the improvement in the record, the position of choristoderes within Diapsida remains uncertain. Some analyses have suggested that choristoderes are basal Archosauromorpha (e.g. Evans, 1988; Gauthier *et al.*, 1988), but others have placed them alternatively as the sister group of Archosauromorpha (e.g. DeBraga and Rieppel, 1997), of Archosauromorpha +Lepidosauromorpha (e.g. Evans, 1988; Gao and Fox, 1998; Dilkes, 1998), or of Euryapsida within an expanded Lepidosauromorpha (e.g. Müller, 2004). Resolution of their phylogenetic position requires a better understanding of the early history of the group, but each of the above hypotheses predicts that choristoderes had separated from their

(undetermined) sister group by the end of the Permian.

Eleven choristoderan genera are currently considered valid. Of these, *Champsosaurus* and *Simoedosaurus* (Late Cretaceous-earliest Eocene, Euramerica), *Ikechosaurus* and *Tchoiria* (Cretaceous, China and Mongolia, Efimov, 1975; Sigogneau-Russell, 1981) are medium-sized (2-5 m total length, skulls up to 700mm from rostral tip to occiput) (Fig. 1), gavialiform reptiles with cordiform skulls, long rostra, and short necks. All recent analyses support the placement of these four genera in a clade, Neochoristodera (Evans and Manabe, 1999; Gao and Fox, 1998; Matsumoto *et al.*, 2007, 2009; Skutchas, 2008). The more basal 'non-neochoristoderes' are smaller (0.3-1.0m) and more diverse in their morphology. *Cteniogenys* (Middle-Late Jurassic, Euramerica, Evans 1990), *Lazarussuchus* (Oligocene-Miocene, Europe, Hecht, 1992; Evans and Klembara, 2005), *Monjurosuchus* (Early Cretaceous, China and Japan, Gao *et al.*, 2000; Matsumoto *et al.*, 2007), and *Philydrosaurus* (Early Cretaceous, China, Gao and Fox, 2005) are essentially lizard-like choristoderes with short necks and either open (*Cteniogenys*) or closed (the other three) lower temporal fenestrae, whereas the Early Cretaceous *Shokawa* (Japan, Evans and Manabe, 1999) and *Hyphalosaurus* (China, Gao *et al.*, 1999), the Hyphalosauridae of Gao *et al.* (2008), are nothosauriform with elongated necks. *Khurendukhosaurus* (Early Cretaceous, Mongolia, Sigogneau-Russell and Efimov, 1984, Skutchas 2008; Matsumoto *et al.*, 2009) is of similar/ or slightly larger size to *Hyphalosaurus* (holotype, IVPP V11075)

(similar in dorsal centrum length but femur twice as long: Matsumoto pers. obs. 2008; Matsumoto *et al.*, 2009), but is known only from fragmentary material and its skull and body shape (long or short necked) are not yet known. The Early Cretaceous Mongolian *Irenosaurus* (Efimov, 1979) is based on isolated postcranial bones that lack sufficient diagnostic characters to differentiate them from *Tchoiria* (Evans and Hecht, 1993; Efimov and Storrs, 2000) and the choristoderan status of the European Triassic *Pachystropeus* (Storrs and Gower, 1993; Storrs *et al.*, 1996) is equivocal. Most recently, the genus *Liaoxisaurus* was named on the basis of a new specimen from the Jiufotang Formation of China (Gao *et al.*, 2005), but it is closely similar to *Ikechosaurus pijiagouensis* from the same horizon and its validity as a distinct taxon is in doubt.

Our concept of Choristodera has thus changed substantially in recent years. As it currently stands, the fossil record of Choristodera suggests there was a gradual Jurassic/ Cretaceous increase in maximum size, coupled with an increase in morphological disparity, particularly with respect to the neck and skull. This resulted in several distinct morphotypes (e.g. small short-necked brevirostrine; small long-necked brevirostrine; large short-necked longirostrine), some of which paralleled those of contemporary crocodiles.

Choristoderes are typically found in association with a diverse freshwater assemblage, most members of which, including choristoderes, survived the end-Cretaceous extinction. However, their presence and their level of morphological diversity in different localities shows con-

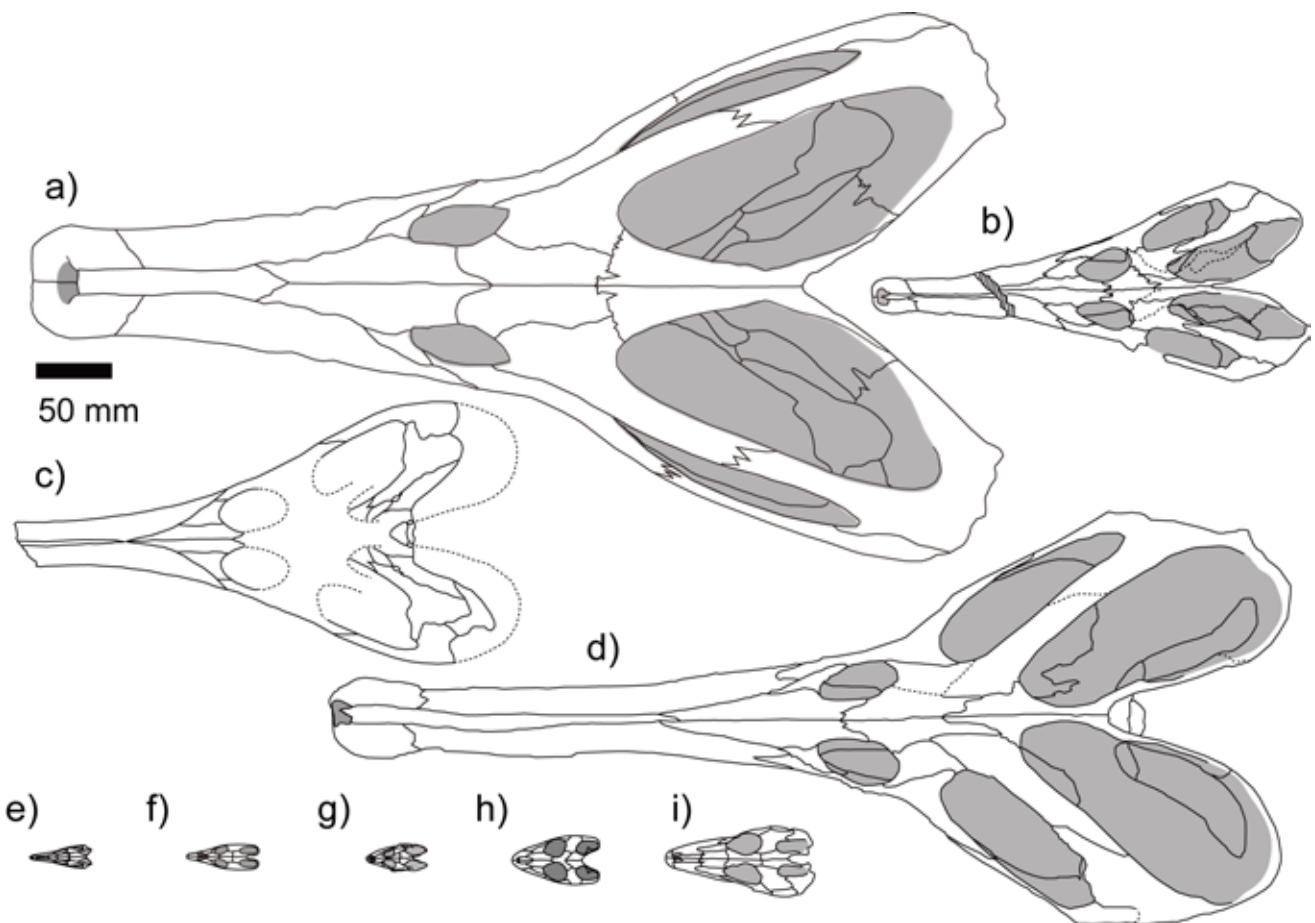


Fig. 1.- Choristoderan skulls drawn to scale: neochoristoderan –a) *Simoedosaurus lemoinei* (modified from Sigogneau-Russell and Russell, 1978) –b) *Ikechosaurus pijiagouensis* (IVPP V13283) –c) *Tchoiria namsarai* (redrawn from Efimov, 1975) –d) *Champsosaurus gigas* (SMM P77.33.24); non-neochoristoderan –e) *Cteniogenys* sp. (Evans, 1990)–f) *Lazarussuchus inexpectatus* (Hecht, 1992) –g) *Hyphalosaurus baitaigouensis* (redrawn from Gao and Ksepka, 2008) –h) *Monjurosuchus splendens* (Matsumoto *et al.*, 2007) –i) *Philydrosaurus proseilus* (Gao and Fox, 2005).

Fig. 1.- Cráneos de Choristodera dibujados a escala: Neochoristodera –a) *Simoedosaurus lemoinei* (modificado de Sigogneau-Russell and Russell, 1978) –b) *Ikechosaurus pijiagouensis* (IVPP V13283) –c) *Tchoiria namsarai* (redibujado a partir de Efimov, 1975) –d) *Champsosaurus gigas* (SMM P77.33.24); non-Neochoristodera –e) *Cteniogenys* sp. (Evans, 1990)–f) *Lazarussuchus inexpectatus* (Hecht, 1992) –g) *Hyphalosaurus baitaigouensis* (redibujado a partir de Gao and Ksepka, 2008) –h) *Monjurosuchus splendens* (Matsumoto *et al.*, 2007) –i) *Philydrosaurus proseilus* (Gao and Fox, 2005).

siderable variation, that may be indicative of underlying biological or ecological signals. Moreover, on current evidence, choristoderes became extinct in the Miocene while other members of the assemblage survived. Here we review choristoderan distribution and diversity from the Jurassic to the Miocene, and offer a preliminary analysis of the possible ecological relationship between choristoderes and other aquatic taxa, notably crocodiles with which they are most often compared.

1.1. Institutional abbreviations

GUI, Guimarota collections, Freie Universität, Berlin, Germany; **IVPP V**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **SMM**, The Science Museum Minnesota, St. Paul, Minnesota, USA; **UALVP**, Laboratory for Vertebrate Paleontology, Department of Biological Science, University of Alberta, Edmonton, Canada.

2. Temporal and geographical distribution

2.1 Triassic

Although the Triassic genus *Pachystropeus* (England, Germany) has been referred to the Choristodera (e.g. Storrs and Gower, 1993; Storrs *et al.*, 1996), it is too poorly known to be attributed with any confidence. The most diagnostic features of choristoderes are in their skulls, and there is no confirmed skull material for *Pachystropeus*.

2.2 Jurassic

The first definitive records of choristoderes are from the Middle Jurassic of Europe and Asia. *Cteniogenys* is a small, probably amphibious, choristodere from the Bathonian of England (e.g. Kirtlington Mammal Bed, Oxfordshire, England, Evans, 1990) and Scotland (Skye, Evans and Waldman, 1996). It is also recorded from the Kimmeridgian of Portugal (Guimarota, Seiffert, 1973; Evans, 1989) and North America (Brushy Basin Member, Morrison Formation, South Dakota, Wyoming and Utah: Gilmore, 1928; Evans, 1990; Chure and Evans, 1998; Foster and Trujillo, 2000). There is unnamed (but broadly similar) material from the Callovian Balambansai Svita, Fergana Basin, of Kyrgyzstan (Averianov *et al.*, 2006). Plotted on a paleoclimate map (Scotese, 2000), most of these records are in relatively warm temperate areas (Fig. 2-a). Although the Morrison Formation falls broad-

ly into the arid climate zone, it covered a huge area and encompassed a range of palaeoenvironments, including wetlands suitable for small aquatic reptiles (Turner and Peterson, 2004). Interestingly, *Cteniogenys* is not evenly distributed through the Morrison (Brushy Basin Member) microvertebrate assemblages (Chure and Evans, 1998). It seems to be most common in the northern part of the formation (most notably at Quarry 9, Como Bluff), representing coastal swamp environments, but rare (Dinosaur National Monument) or absent (Fruita Paleontological area) on the Colorado Plateau (interior continental water bodies) (Chure and Evans, 1998). This may be significant because the British Bathonian localities and Guimarota both represent coastal freshwater-brackish lagoonal environments (e.g., Schudack, 2000), and the Balambansai Svita of the Fergana Depression has been described as transitional from terrestrial to marginal marine (Averianov *et al.*, 2005).

2.3 Lower Cretaceous

Fossil deposits in the Lower Cretaceous of Asia (Eastern Russia, Inner Mongolia, China, Japan) have yielded the greatest known choristodere diversity, with at least seven recorded genera representing all known choristoderan morphotypes (Fig. 2-b): the long-necked Japanese *Shokawa* (Evans and Manabe, 1999) and Chinese *Hypalosaurus* (Gao *et al.*, 1999; Ji *et al.*, 2004; Gao and Ksepka, 2008); the longirostrine gavial-like neochoristoderes *Tchoiria* (Mongolia, Efimov, 1979) and *Ikechosaurus* (Mongolia, China, Brinkman and Dong, 1993; Liu, 2004); the small lizard-like *Monjurosuchus* (China, Japan, Gao *et al.*, 2000; Matsumoto *et al.*, 2007) and *Philydrosaurus* (China, Gao and Fox, 2005; Gao *et al.*, 2007); and the problematic *Khurendukhosaurus* (Mongolia, Sigogneau-Russell and Efimov, 1984; Skutschas, 2008; Matsumoto *et al.*, 2009). At this time, Eastern Eurasia was divided into two paleophytogeographic provinces: a northern Siberian-Canadian Region (Vakhrameev, 1978), with Tetori-type floras at its southern margin (Kimura, 1979) and a temperate to humid climate; and a southern Euro-Sinian Region (Vakhrameev, 1978) with Ryoseki-type floras (Kimura, 1979) and a suggested subtropical to tropical climate, with an annual dry season. All major choristodere localities occur in the northern province, in continental wetland (e.g. Kuwajima and Okurodani formations), fluvial (e.g. Khuren Dukh) or lacustrine (e.g. Yixian Formation) environments; they have not been reported from the southern province (e.g. the semi-arid fluvial ecosystem of the Khorat Group in Thailand [Meesook, 2000]), although several semi-aquatic fresh-

water crocodiles (goniopholidids *Sunosuchus*, *Goniopholis*, and *Siamosuchus*, and the neosuchian *Khoratosuchus*) are known from the area (e.g. Lauprasert *et al.*, 2009).

The Lower Cretaceous record for the rest of Laurasia is restricted to a partial femur, possibly neochoristoderan, from the Barremian Yellow Cat Member of the Cedar Mountain Formation of Utah (Britt *et al.*, 2006). Palaeoenvironmental reconstructions for the Yellow Cat Formation (Kirkland *et al.*, 1999) suggest a semiarid monsoonal environment, but one with enough standing water to support a stable freshwater community. The overlying Mussentuchit Formation contains a more diverse tetrapod assemblage, but there is no record of choristoderes.

2.4 Upper Cretaceous

In sharp contrast to the Lower Cretaceous, there is currently no record of choristoderes in the Upper Cretaceous of East Asia. This may reflect a lack of suitable depositional environments. Most Late Cretaceous fossil reptiles from China and Mongolia come from arid terrestrial environments. For choristoderes, the focus shifts to North America where there are abundant records of the gavial-like neochoristodere *Champsosaurus* in Utah, Wyoming, Montana, North Dakota, Alberta, Saskatchewan and the Canadian Arctic (Fig. 2-c). These localities, including those of the Arctic (Tarduno *et al.*, 1998; Vandermark *et al.*, 2007), were mostly located in low-lying river channels and deltaic deposits bordering the Western Interior Seaway; the climate was warm. This distribution may represent an ecological preference, or simply a prevalence of this type of environment within the Late Cretaceous rock record (e.g. Markwick, 1998). Putative records of non-neochoristoderes are limited to the Oldman and the Dinosaur Park formations, Alberta (Irvine locality and Dinosaur Provincial Park). These small specimens were assigned to *Cteniogenys* (Gao and Fox, 1998), but the material (incomplete dentaries and maxillae) is not sufficiently complete or diagnostic for generic identification (Matsumoto *et al.*, 2009), especially with such a large age gap.

A single vertebra from the Lower Campanian of Austria (Gosau Beds, Muthmannsdorf; Buffetaut, 1989) demonstrates the presence of choristoderes in the Late Cretaceous of Europe. The fossil bearing horizon has been interpreted as a brackish estuarine environment (Sachs and Hornung, 2006), with a humid, paratropical climate (Herman and Kvacek, 2007). Given the rarity of the choristodere material in the deposit, it may have been

transported from further upstream.

2.5 Paleocene to Miocene

Champsosaurus survived the end-Cretaceous extinction and in the Paleocene was joined by another neochoristodere, *Simoedosaurus*. Conditions were temperate and neochoristoderes continued to be well represented in North America (Fig. 3-a), with limited European and Asian records. In Europe, *Champsosaurus* and *Simoedosaurus* have been recorded from littoral and infralittoral deposits at Erquelinnes, Belgium (Sigogneau-Russell and de Heinzelin, 1979) and from Mont Berru, France (Sigogneau-Russell and Russell, 1978; Sigogneau-Russell, 1985), respectively, and there is undescribed material of *Champsosaurus* from the latter locality (Matsumoto pers. obs. 2008). Postcranial elements of *Simoedosaurus* have also been reported from Upper Paleocene-Early Eocene coastal deposits (Dzhylyga 1a-1b) in southern Kazakhstan (Averianov, 2005), where conditions were warmer and more humid.

In North America, the faunal transition from the Paleocene to the Eocene (Clarkforkian-Watsachian) has been well studied in continuous sections such as those of the Bighorn Basin, Wyoming (Bartels, 1983; Gunnell *et al.*, 1993). Choristodere material is abundant in the Tiffanian and early Clarkforkian horizons in the Fort Union Formation of Wyoming, but is quite rare in the younger (early Eocene, Watsachian) Willwood Formation. Bartels (1983) attributed this decline to local effects (a reduction in the number and size of the streams), but this was also an interval of major faunal change associated with elevated temperatures. These are also the last records of neochoristoderes, and may mark the extinction of the clade (Gingerich, 2000; Gunnell *et al.*, 1993; Bartels, 1983). However, non-neochoristoderes, having effectively disappeared from the record in the Early Cretaceous, unexpectedly reappeared in the Paleogene of Europe (France, Germany, Czech Republic) in the form of the small, lizard-like *Lazarussuchus* (Hecht, 1992; Evans and Klembara, 2005; Böhme, 2008; Evans *et al.*, unpublished). These small reptiles were in continental lake environments. Their last record in Europe is from the Lower Miocene of the Czech Republic, in a warm (subtropical) wet environment (Fig. 3-b).

In summary, Choristodera were distributed throughout Laurasia from the Jurassic to the Miocene in warm temperate-paratropical localities. However, the group is notably absent or poorly represented in some localities and time periods, for example the Lower Cretaceous of Europe and the Upper Cretaceous of Asia. As so often with

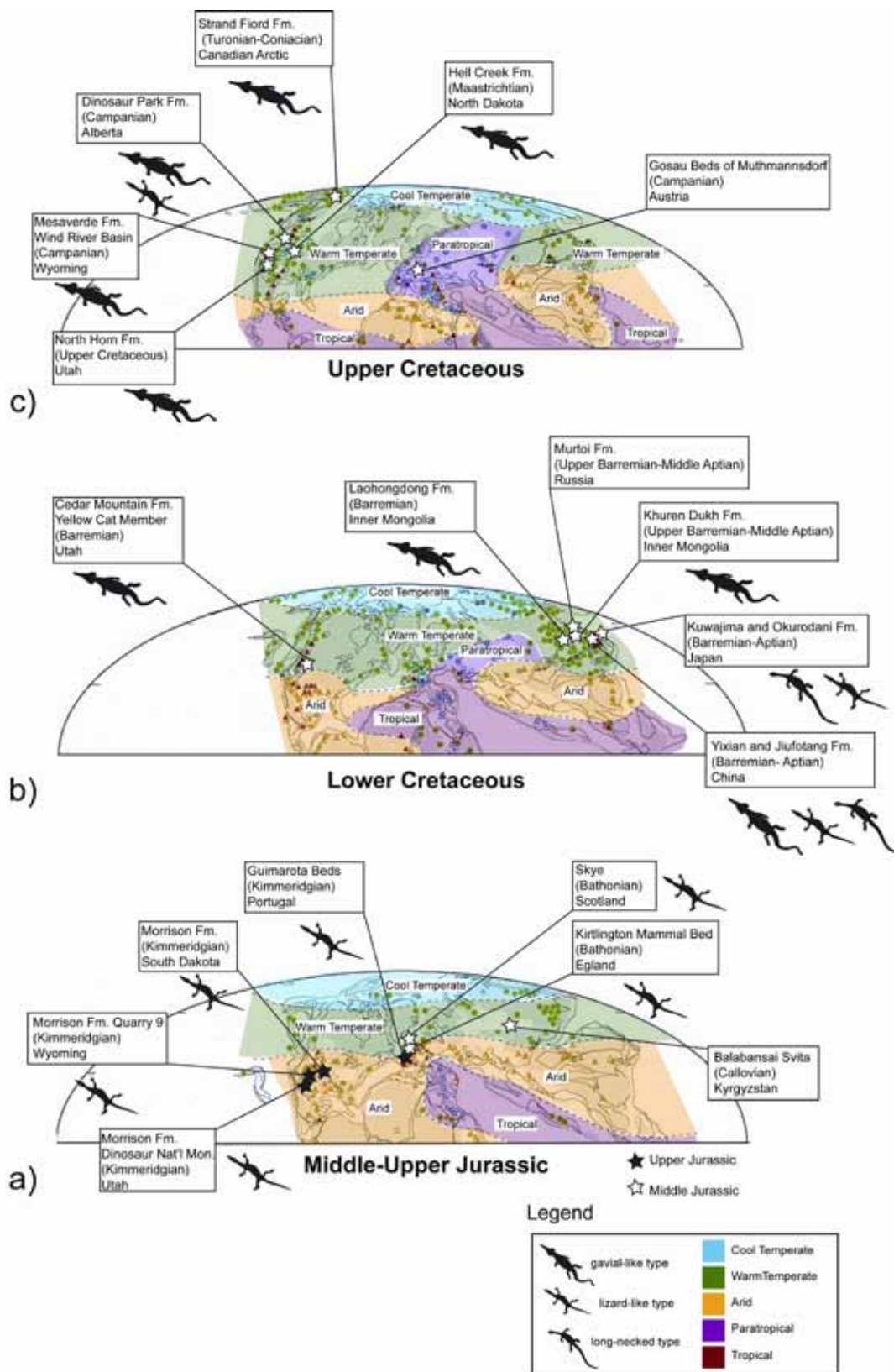


Fig. 2.- Paleogeographical distribution of Choristodera during the Mesozoic: plotted on climate history maps (modified from Scotese, 2002). -a) Middle-Upper Jurassic. -b) Lower Cretaceous. -c) Upper Cretaceous.

Fig. 2.- Distribución paleobiogeográfica de Choristodera durante el Mesozoico en relación con los mapas de la historia climática modificado de Scotese (2002). -a) Jurásico Medio-Superior. -b) Cretácico Inferior. -c) Cretácico Superior.

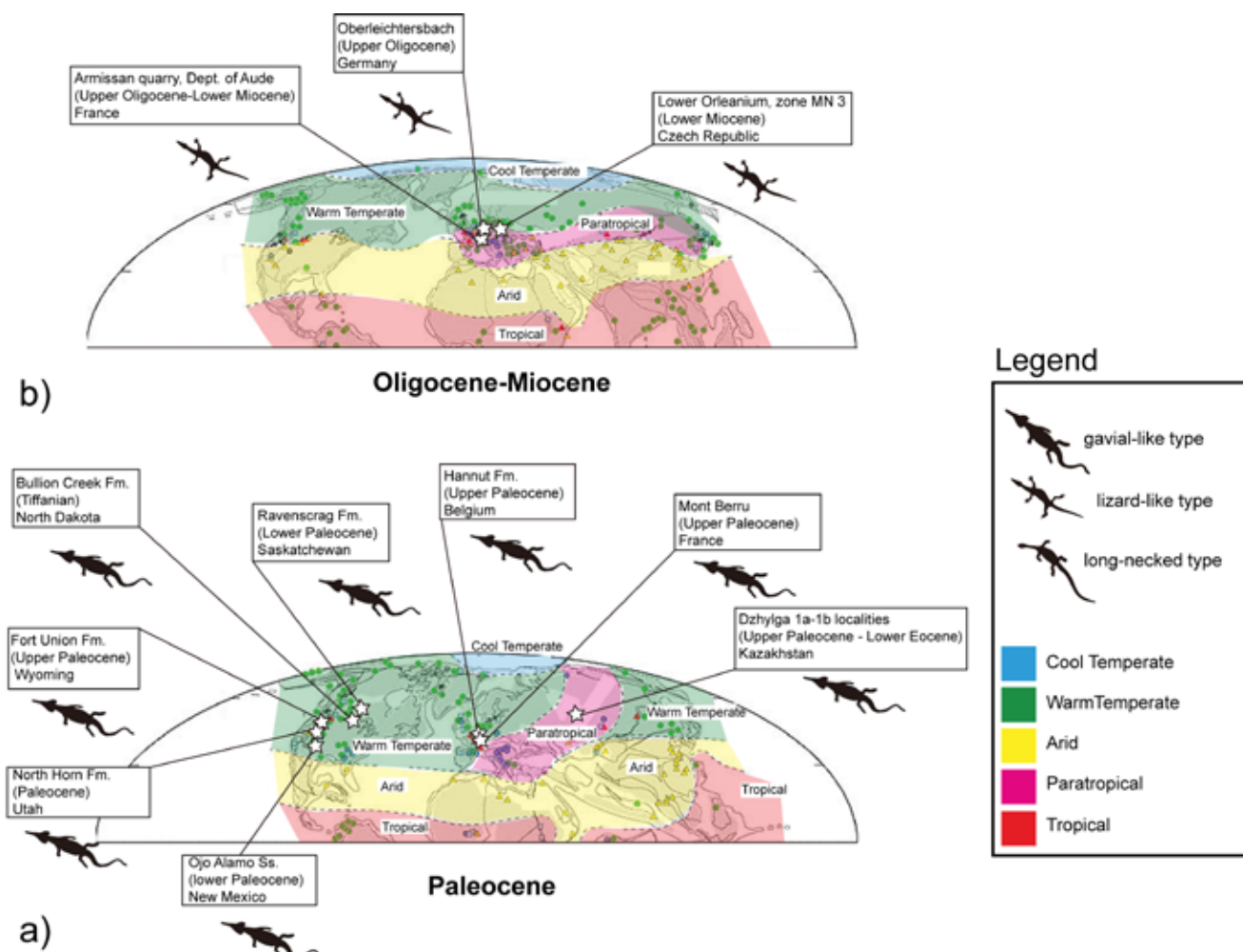


Fig. 3.- Paleogeographical distribution of Choristodera during the Cenozoic: plotted on climate history maps (modified from Scotese, 2002). -a) Paleocene. -b) Oligocene-Miocene.

Fig. 3.- Distribución paleogeográfica de Choristodera durante el Cenozoico en relación con los mapas históricos climáticos modificados de Scotese (2002). -a) Paleoceno. -b) Oligoceno-Mioceno.

the fossil record, the challenge is to determine whether these absences are simply an artifact of sampling, preservation and taphonomy, or are real absences that require explanation and may provide an insight into the biology, lifestyle, or ecological interactions of the group.

3. Faunal associations and ecological relationships with crocodiles

3.1. Assemblage composition

A comparison of well-known Mesozoic to Cenozoic assemblages (Fig. 4) demonstrates that choristoderes occur in mesic depositional environments that are rich in vertebrates, especially fresh water and amphibious animals such as fish, frogs, salamanders, turtles and crocodiles (Fig. 4-a). Typically, these assemblages contain a greater

diversity of crocodiles than choristoderes (Fig 5; Table 2-4) although they did not necessarily all live together. For example, the North Horn Formation (Upper Cretaceous-Lower Paleocene, Utah, USA) has reportedly yielded five crocodile taxa (possibly an overestimate as the count is based on isolated teeth) and one choristodere. However, representatives of the two groups are found in different localities (Cifelli *et al.*, 1999a) and this may reflect differences in habitat preference/tolerance or, possibly, some form of competitive exclusion. Similarly, six crocodiles have been recorded from the Morrison Formation (Fig 5; Table 2), with one small choristodere (*Cteniogenys*), but three of the crocodiles (the 'Fruita crocodile', *Hallopus*, and *Hoplosuchus*) are basal forms that were mainly or fully terrestrial and come from localities on the Colorado Plateau where *Cteniogenys* is rare or absent. In addition, several very productive horizons/localities in the

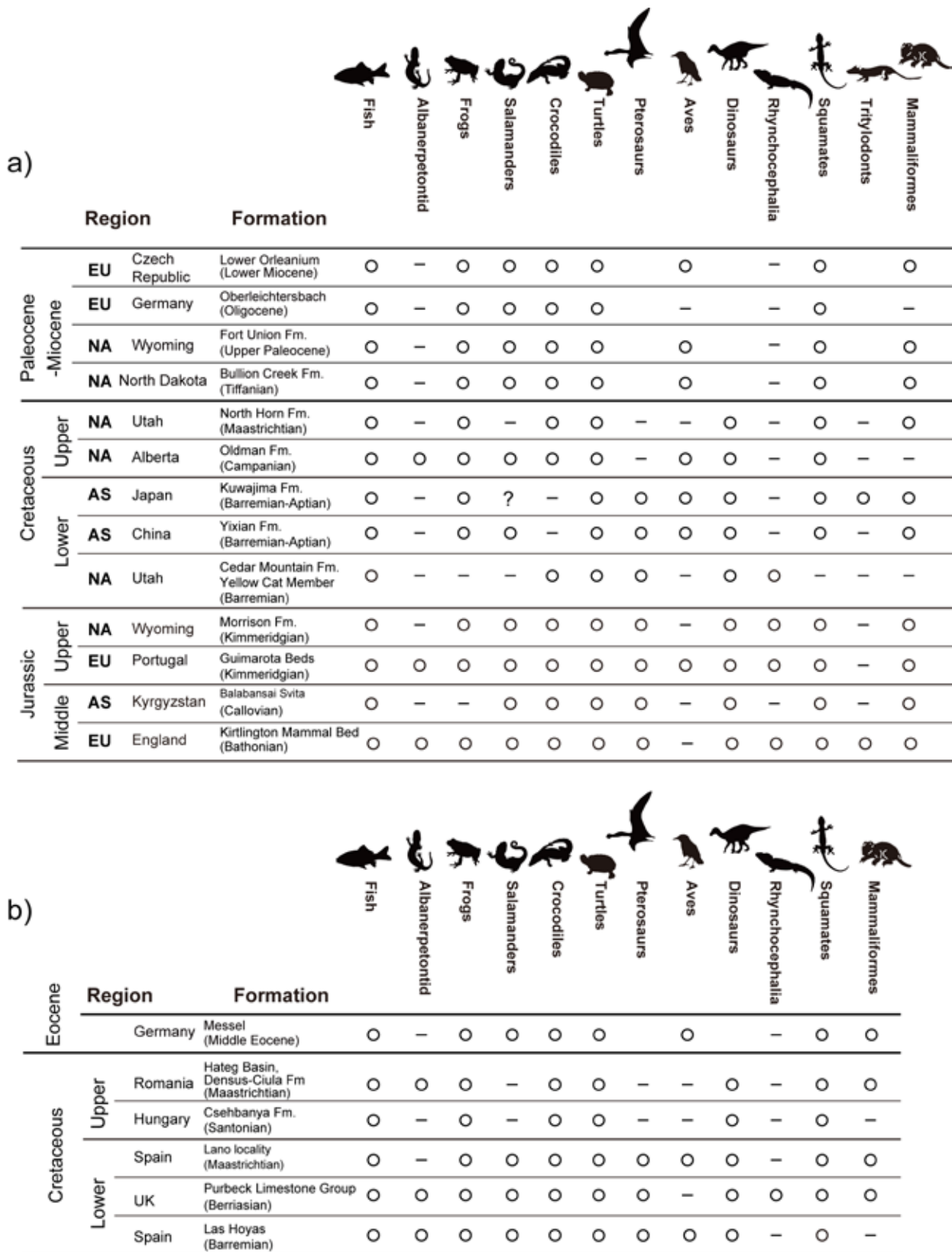


Fig. 4.- Assemblage composition through the Mesozoic and Cenozoic. -a) well studied choristoderan localities -b) European microvertebrate localities where choristoderes are not known.

Fig. 4.- Composición de las asociaciones a lo largo del Mesozoico y Cenozoico. -a) localidades bien estudiadas con coristoderos. -b) localidades Europeas con microvertebrados donde no se han registrado coristoderos.

Cretaceous and Eocene of Europe yield crocodiles but no choristoderes (Fig. 4-b) despite an otherwise generally similar associated freshwater fauna. These include: the Purbeck Limestone Group (Berriasian) of England (three valid crocodile genera, e.g. Salisbury, 2002); the limestones of the La Huerquina Formation (Barremian) at Las Hoyas, Spain (at least five crocodile genera, Ortega *et al.*, 1999, Buscalioni and Fregenal-Martínez, 2006); and the Wessex Formation (Barremian) of England (eight crocodile genera, Sweetman, 2009, but based mainly on teeth);

as well as the Middle Eocene beds of Messel, Germany (seven crocodile genera, Morlo *et al.*, 2004).

By contrast, in those Lower Cretaceous Asian horizons that contain the greatest diversity of choristoderes (e.g. Yixian Formation, China; Kuwajima and Okurodani formations, Japan; Fig. 5; Table 4), crocodiles are conspicuously absent. Whether this is an ecological or temporal phenomenon is not clear, as possible goniopholid crocodile remains have been reported (Azuma, 2003), from the somewhat drier (Yabe *et al.*, 2003) late Hauterivian to

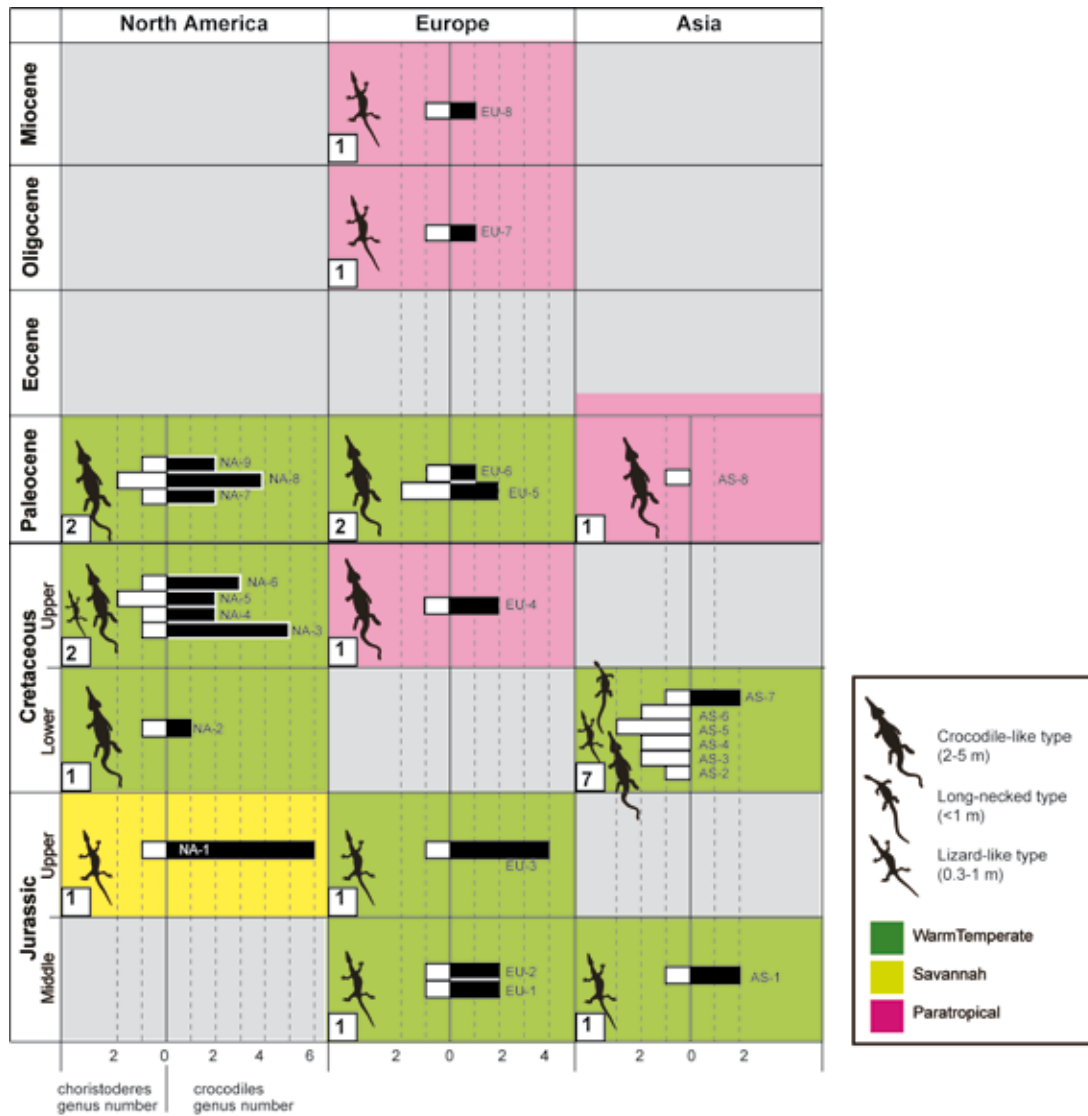


Fig. 5.- Comparison of relative numbers of choristoderes and crocodiles (genera). Each bar indicates one horizon: choristoderes are in white and crocodiles in black. The horizon number corresponds to that in table 2-4: North America (NA) 1-9 in Table 2; Europe (EU) 1-9 in Table 3; Asia (AS) 1-8 in Table 4. The number in the left hand corner of each box indicates the total number of choristoderes genera for that region and period.

Fig. 5.- Comparación entre el número relativo de coristoderes y de cocodrilos (géneros). Cada barra indica un horizonte: coristoderes se representan en blanco y cocodrilos en negro. El número del horizonte corresponde a los que se expresan en la tabla 2-4: Norte America (NA) 1-9 en la Tabla 2; Europa (EU) 1-9 en la Tabla 3; Asia (AS) 1-8 en la Tabla 4. El número en el extremo izquierdo de cada caja indica el número total de géneros de coristoderes para esa región y periodo.

	Region	Choristoderes	Skull	Size	References	Region	Crocodyles	Skull	Size	References		
Miocene-Upper Oligocene	EU	<i>Lazarussuchus</i>	0.05 m	0.3 m	Hecht, 1992	EU	<i>Diplocynodon</i>		0.3-1.5 m	Piras and Buscalioni, 2006		
Paleocene	NA	<i>Champsosaurus gigas</i>	0.49 m	3.5 m	Erickson, 1985	NA	<i>Leidyosuchus</i>		4 m	Erickson, 1982		
	EU	<i>C. dolloi</i>	0.65 m	4 m	Sigogneau-Russell and Heinzelin, 1979	NA	<i>Wannaganosuchus</i>		1 m	Erickson, 1982		
	NA	<i>Simoedosaurus dakotensis</i>	0.71 m	5 m	Erickson, 1987	NA	<i>Ceratosaursuchus</i>	0.23 m	2 m	Bartels, 1984		
	EU	<i>Simoedosaurus</i> sp.	0.52 m	4 m	SMNS 59026	NA	<i>Allognathosuchus</i>	0.24 m	2 m	Simpson, 1930		
Cretaceous	Upper	NA	<i>Champsosaurus natator</i>	0.5 m	3.6 m	Russell, 1956	NA	<i>Brachychampsia montana</i>	0.39 m	3 m	Norell et al., 1994	
			<i>C. laramiensis</i>	0.41 m	3.0 m	Brown, 1905	NA	<i>Leidyosuchus sternbergi</i>	0.34 m	3 m	Brochu, 1997	
			<i>C. ambulator</i>	0.4 m	3 m	Brown, 1905	NA	<i>Thoracosaurus neocasiensis</i>		2.5 m	Brandalise de Andrade, personal communication, August 2009	
	Lower	AS	<i>Ikechosaurus pijiagoensis</i>	0.27 m	1.7 m	Liu, 2004	AS	<i>Theriosuchus</i>		0.5 m	Schwarz and Salisbury, 2005	
		AS	<i>Tchoiria namsarai</i>	0.3 m	2 m	undescribed material	AS	<i>Shantungosuchus</i>		0.3 m	Wu et al., 1994	
		AS	<i>Khurendkuhosaurus</i>	?	1 m?	Matsumoto et al., 2009						
		AS	<i>Philydrosaurus proseilus</i>	0.1 m	< 1 m?	Gao et al., 2007						
		AS	<i>Monjurosuchus splendens</i>	0.06 m	~0.5 m	Gao and Li, 2006; Gao et al., 2000						
		AS	<i>Hyphalosaurus lingyuanensis</i>	0.06 m	1 m	Holotype (IVPP V11705)						
		AS	<i>Shokawa ikoi</i>	?	> 0.6 m	Evans and Manabe, 1999						
	Jurassic	Middle-Upper	EU	<i>Ctenioenys</i> sp.	0.04 m	~0.3 m	Evans, 1990	EU	<i>Macelognathus</i>		3 m	Hups et al., 2005
			/NA				EU	<i>Machimosaurus</i>		9.5 m	Charig, 1976	
						EU/NA	<i>Goniopholis</i>		3 m	Schwarz and Salisbury, 2005		
						EU	<i>Lusitanisuchus</i>		0.4 m	Schwarz and Fehner, 2008		
						EU	<i>Theriosuchus</i>		0.5 m	Schwarz and Salisbury, 2005		
						EU	<i>Eutretauranosuchus</i>		3 m	Hups et al., 2005		
						NA	<i>Hoplosuchus kayi</i>		0.2 m			
						NA	<i>Hallopus victor</i>		0.6 m	Walker, 1970		
						NA	" <i>Fruitachamysa</i> "		1 m			
						AS	<i>Sunosuchus</i> sp.	0.42 m	3 m	Schellhorn et al., 2009		

Table 1.- Estimated total length (skull to tail tip) for choristoderes and crocodiles

Tabla 1.- Longitud total estimada (cráneo a cola) para coristoderos y cocodrilos.

late Aptian Kitadani Formation (e.g. Kusuhashi, 2008; Tsubamoto, 2004), which overlies the choristodere bearing Kuwajima and Okurodani formations in Japan (e.g. Fujita, 2003; Kusuhashi, 2008). To date, only one Asian horizon (the Barremian Laohongdong Formation, Inner Mongolia) is known to contain both choristoderes (*Tchoiria*) and crocodiles. Sha *et al.* (2006) report that crocodiles were also found in the Khuren Dukh Formation (Mongolia), but no further data is available and Averianov and Skutchas (2000) do not include crocodiles in their faunal list for this formation. Significantly, Buscalioni *et al.* (2003) have reported that the Cretaceous crocodile fauna of Asia was dominated by basal groups (protosuchids, gobisuchids, ziphosuchians) that were largely terrestrial in their habits.

3.2 Comparison of size and rostral morphology in crocodiles and choristoderes

Based on Table 1, Tables 2-4 present comparisons of body size for crocodiles and choristoderes in selected horizons where they co-occur; Fig. 6 compares rostral

morphologies in the same horizons. Body size estimates (total length: tip of snout to tail tip) are taken mainly from the literature, as listed. However, where body size data is lacking, size has been estimated for crocodiles based on skull/body length ratios for extant *Crocodylus* (Wermuth, 1964; Bellairs, 1969), and for choristoderes based on the proportions of a complete articulated skeleton of the neochoristodere *Ikechosaurus pijiagouensis* (IVPP V13283, Liu, 2004) with a head:body ratio of 1:6.2 (Table 4). As skull morphology and size change ontogenetically in crocodiles (Dodson, 1975), the skulls used in these estimates were restricted to mature specimens.

Jurassic

Early choristoderes were small. In most Jurassic horizons where choristoderes and crocodiles are found together (e.g. Middle Jurassic of UK and Kyrgyzstan; Upper Jurassic of Portugal, North America), the adult crocodiles (mainly goniopholids but also atoposaurids) are up to ten times larger (~ 2.5-3.0 m) than the choristoderes (*Ctenioenys*: ~0.3-0.5 m). Recently discovered choristodere vertebral centra from the Balanbasai Svita, Fergana (Mid-

North America	Horizon No.	Formations	Skull No.	Choristoderes	Size	Skull No.	Crocodyles	Size	References			
Paleocene	NA-9	North Dakota		<i>Champsosaurus gigas</i>	3.5 m		<i>Leidyosuchus formidabilis</i>	3-4 m	Erickson, 1999			
		Bullion Creek Fm. (Tiffanian)		<i>Champsosaurus</i> sp.	3-4 m		<i>Wannaganosuchus brachymanus</i> possibly juvenile of <i>Allognathosuchus</i> (Lucas and Estep, 2000)	1 m				
	NA-8	Wyoming	Fort Union Fm. (Upper Paleocene)	ch-10	<i>Champsosaurus gigas</i>	3.5 m	cr-22	<i>Allognathosuchus</i> (e.g. <i>A. heterodon</i>)	2 m	Bartels, 1983		
				ch-9	<i>Simoedosaurus</i> sp.	4-5 m	cr-21	<i>Leidyosuchus formidabilis</i>	4 m			
							cr-20	<i>Ceratopsuchus burdoshi</i>	2 m			
							cr-19	(<i>Diplocynodon</i> sp.)	0.3-1.5 m			
	NA-7	Utah	North Horn Fm. (Paleocene)		<i>Champsosaurus</i>	3-4 m		<i>Allognathosuchus</i>	2 m	Cifelli et al., 1999a		
								<i>Leidyosuchus</i>	4 m			
	Cretaceous	Upper	NA-6	North Dakota	Hell Creek Fm. (Maastrichtian)	ch-7	<i>Champsosaurus</i> sp.	cr-17	<i>Brachychampsia montana</i>	3 m	Pearson et al., 2002	
								cr-16	<i>Leidyosuchus sternbergi</i> (= <i>Borealosuchus</i> ; Brochu, 1997)	3-4 m		
cr-15								<i>Thoracosaurus neocesariensis</i>	2.5 m			
NA-5		Alberta	Dinosaur Park Fm (Campanian)		<i>Champsosaurus natator</i> non-Neochoristodera	3-4 m		<i>Leidyosuchus canadensis</i> <i>Albertochampsia langstoni</i>	3 m	Brinkman, 1990 Gao and Brinkman, 2005 Wu, 2005		
						?						
NA-4		Wyoming	Mesaverde Fm. Wind River Basin (Campanian)		<i>Champsosaurus</i> sp.	3-4 m		<i>Leidyosuchus</i> sp. Alligatorinae	3-4 m ?	DeMar and Breithaupt, 2008		
NA-3		Utah	North Horn Fm. (Upper Cretaceous)		<i>Champsosaurus</i> sp.	3-4 m		? Atoposauridae gen. and sp. Indet. gen. and sp. Indet. ? Pholidosauridae <i>Leidyosuchus</i> sp. <i>Allognathosuchus</i>	? ? ? ? 3-4 m 2 m	Cifelli et al., 1999a		
Lower	NA-2	Utah	Cedar Mountain Fm. Yellow Cat Member (Barremian)	ch-5	Neochoristodera indet.	?	cr-12	Crocodylia indet.	? ? ?	Britt et al., 2009 Britt et al., 2006 Kirkland et al., 1999		
Jurassic	Upper	NA-1	Wyoming	Morrison Fm. (Kimmeridgian)	ch-3	<i>Cteniogenys antiquus</i>	0.3 m	cr-8	<i>Goniopholis</i> sp.	3 m	Clark, 1994	
								cr-7	<i>Hoplosuchus kayi</i>	0.2 m		
								cr-6	<i>Hallopus victor</i>	0.6 m		Göhlich, et al., 2005
								cr-5	<i>Macelognathus vagans</i>	3 m		
									<i>Eutretauranosuchus</i> "Fruitachampsia"	2 m 1 m		

Table 2.- List of choristoderan localities/horizons with crocodiles in North America

Tabla 2.- Lista de localidades/horizontes de coristoderos con cocodrilos en Norte América.

de Jurassic), Kyrgyzstan (Averianov *et al.*, 2006), are of a similar size and morphology to those of *Cteniogenys* from the Morrison Formation, North America (Foster and Trujillo, 2000). Although, the body proportions of this Asian choristodere are still unknown, the total length would have been less than 1 m even if it was long-necked (by comparison with the largest specimens of the Lower Cretaceous *Hyphalosaurus* IVPP V11075). Two crocodiles are known from the Balanbasai Svita (Averianov *et al.*, 2006). The first, the neosuchian *Sunosuchus*, has a total length of about 2.5 m. The other is an undetermined thalattosuchian of unknown length. At Guimarota, Portugal, the Kimmeridgian lignites have yielded several crocodiles (Martin and Krebs, 2000). The largest is the longirostrine *Machimosaurus*, about 30 times the size of *Cteniogenys*, but this is an open sea crocodile (Krebs, 1967). Three crocodiles are of similar length to *Cteniogenys*: the poorly known *Lusitanisuchus* (0.4 m) (Schwarz and Fechner, 2008), *Lisboasaurus estesi* and the atoposaurid *Theriosuchus* (Schwarz and Salisbury, 2005: 0.5 m). These three are relatively brevirostrine crocodiles (rostral length/ basal skull length ~ 50%), not dissimilar

in overall skull shape to *Cteniogenys* (Evans, 1990), but they are primarily terrestrial. The Morrison Formation is similar, with both large aquatic crocodiles (up to 3 m: *Eutretauranosuchus*, *Goniopholis* spp., *Macelognathus*) and smaller terrestrial ones (0.2-1.0 m: *Hallopus victor*, *Hoplosuchus kayi*, and the 'Fruita crocodile') (Clark, 1994; Chure *et al.*, 1998; Göhlich *et al.*, 2005; Hups *et al.*, 2005).

Lower Cretaceous

Crocodile teeth and osteoderms are recorded from the Yellow Cat Member of the Cedar Mountain Formation, in conjunction with the choristodere femur recorded above (Britt *et al.*, 2006). A more diverse crocodile assemblage is known from the overlying Mussentuchit Formation (Cifelli *et al.*, 1999b), but without choristoderes. The Barremian Laohongdong Formation, Inner Mongolia, is currently the only Lower Cretaceous deposit in Asia yielding both choristoderes (the large gavial-like *Ikechosaurus sunailinae*) and crocodiles (the protosuchian *Shantungosuchus*, 0.3 m: Wu *et al.*, 1994; and the atoposaurid cf. *Theriosuchus* sp., 0.5 m: Wu *et al.*, 1996, known also from

Europe	Horizon No.	Formations	Skull No.	Choristoderes	Size	Skull No.	Crocodyles	Size	References	
Oligocene-	EU-9	Czech Republic	ch-14	<i>Lazarussuchus davoraki</i>	0.3 m	cr-25	<i>Diplocynodon</i> sp.	0.3-1.5 m	Evans and Klembara, 2005	
Miocene		Lower Orléanum, zone MN 3 Formation (Lower Miocene)								
		France Armissan quarry (Upper Oligocene-Lower Miocene)		<i>Lazarussuchus inexpectatus</i>	0.3 m		?		Hecht, 1992	
	EU-7	Germany Oberleichtersbach (Upper Oligocene)	ch-13	<i>Lazarussuchus</i> sp.		cr-24	<i>Diplocynodon</i> sp.	0.3-1.5 m	Böhme, 2008	
Paleocene	EU-6	Belgium Hannut Fm. (Upper Paleocene)	ch-11	<i>Champsosaurus dolloi</i>	4 m	cr-23	<i>Eosuchus leichei</i>	3.5 m	Delfino et al., 2005	
	EU-5	France		<i>Simoedosaurus lemoinei</i>	4 m		<i>Asiatosuchus</i> sp.	>4 m	Sigogneau-Russell, 1985	
		Mont Berru		<i>Champsosaurus</i>	3-4 m		<i>Borealosuchus</i> sp.		Prasad and F de Lapparent de Borin, 2002 Martin, 2008	
Cretaceous	Upper	EU-4	Lower Austria	ch-8	Choristodera indet.		<i>Doratodon carcharidens</i>	?	Sachs and Hornung, 2006	
			Gosau Group Lower Campanina				cr-18	Alligatoridae indet.	?	Buffetaut, 1979
Jurassic	Upper	EU-3	Portugal Guimarota Beds (Kimmeridgian)	ch-4	<i>Cteniogenys</i> sp.	0.3 m	cr-11	<i>Machimosaurus</i>	9.5 m	Evans and Chure, 1998
							cr-10	<i>Goniopholis</i>	3 m	Martin and Krebs, 2000
							cr-9	<i>Lusitanisuchus</i>	0.4 m	
	Middle	EU-2	England Kirtlington Mammal bed (Upper Bathonian)	ch-1	<i>Cteniogenys</i> sp.	0.3 m	cr-2	Goniopholididae (cf. <i>Nannosuchus</i> =?juvenile <i>Goniopholis</i>)	?	Evans and Milner, 1994
							cr-1	Atoposauridae	?	
	EU-1	Scotland Skye (Upper Bathonian)		<i>Cteniogenys</i> sp.	0.3 m		Atoposauridae Goniopholididae	? ?	Evans and Waldman, 1996	

Table 3.- List of choristoderan localities/horizons with crocodiles in Europe

Tabla 3.- Lista de localidades/horizontes de coristoderos con cocodrilos en Europa.

Guimarota [see above]). Isolated larger (mature) specimens of *I. sunailinae* (e.g. IVPP V 1596.5) from the Laolonghuo locality (Brinkman and Dong, 1993) are similar in size (centrum length 18.4 mm at cervical [C]3) to the adult of *Ikechosaurus pijiagouensis* (Liu, 2004) from the Jiufotang Formation of China (centrum length 17-18 mm through C2-C9; 1.7 m total body length). Thus, in the one Asian locality where crocodiles and choristoderes are known to co-occur, the choristoderes appear to have been larger. Moreover, as protosuchids and atoposaurids are considered to be primarily terrestrial (Brinkman, 1989; Schwarz and Salisbury, 2005; Wu et al., 1994), the two groups had different niches.

Upper Cretaceous

The isolated choristoderan vertebra from the Gosau Group of Muthmannsdorf (Lower Austria) is about 15 mm in length. This equates to a body length of about 2 m, assuming neochoristoderan proportions (e.g. *Ikechosaurus pijiagouensis*: presacral centrum length 17-20 mm, total length ~2.0 m). The Gosau bone bed has also yielded two crocodiles, the ziphosuchian *Doratodon* (Company et

al., 2005) and Alligatoridae indet. (Buffetaut, 1979). At Muthmannsdorf, *Doratodon* is known only from cranial elements but there have been recent discoveries of the same genus from other localities and formations (Grigorescu et al., 1999; Company et al., 2005). It is a small, probably terrestrial ziphosuchian, possibly similar to the genus *Bergisuchus* in having a tall short-snouted skull (Company et al., 2005).

In North America, *Champsosaurus* is common at many localities and is typically found with more aquatic crown-group crocodylians, most usually the similar-sized *Leidyosuchus* (some species of which have been placed in the genus *Borealosuchus*, Brochu, 1997). The two differ, however, in rostral morphology and thus, presumably, feeding habit. *Champsosaurus* has a long slender rostrum whereas that of *Leidyosuchus-Borealosuchus* is wider and has been described as 'generalised' (Brochu, 2001). In the Hell Creek Formation (Maastrichtian) of southwestern North Dakota and northwestern South Dakota, crocodiles with a wider range of rostral shapes are found with *Champsosaurus* (Pearson et al., 2002). The closest match is the longirostrine gavialoid *Thoracosaurus* (e.g.

Asia	Horizon No.	Formations	Skull No.	Choristoderes	Size	Skull No.	Crocodyles	Size	References	
Paleocene-Eocene	AS-8	Kazakhstan	ch-12	<i>Simoedosaurus</i> sp.	4-5 m			4-5 m	Averianov, 2005	
		Dzhylga 1a-1b Upper Paleocene- Early Eocene								
Cretaceous	Lower	AS-7	Inner Mongolia	ch-6	<i>Ikechosaurus sunailinae</i>	1.7 m	cr-14	<i>Theriosuchus</i>	0.5 m	Wu et al., 1996
			Laohongdong Fm. (Barremian)				cr-13	<i>Shantungosuchus</i>	0.3 m	Wu et al., 1994 Brinkman and Dong, 1993
	AS-6	Inner Mongolia		<i>Tchoiria namsarai</i>	2 m				Efimov, 1975	
		Khuren Dukh Fm. (Barremian- middle Aptian)		<i>Khurendukhosaurus orlovi</i>	1 m?				Sigogneau-Russell and Efimov, 1984	
	AS-5	Russia		<i>Khurendukhosaurus</i> sp.	1 m?				Averianov and Skutschas, 2000	
		Murtoi Fm. (Upper Barremian- middle Aptian)								
	AS-4	China		<i>Ikechosaurus pijagoensis</i>	1.7 m				Liu, 2004	
		Jiufotang Fm. (Aptian)		<i>Philydosaurus proseilus</i> <i>Hyphalosaurus baitaigouensis</i> <i>? Liaoxisaurus chaoyngensis</i>	<1 m ? 1 m				Gao and Fox, 2005 Ji et al., 2004 Gao et al., 2005	
		Yixian Fm. (Barremian)		<i>Monjurosuchus splendens</i> <i>Hyphalosaurus lingyuanensis</i>	0.5 m 1 m				Gao et al., 2000 Gao et al., 1999	
			Japan		<i>Shokawa ikoi</i> <i>Monjurosuchus</i> sp.	>0.6 m				Evans and Manabe, 1999 Matsumoto et al., 2007
AS-3	Okurodani Fm. Barremian-Aptian									
AS-2	Japan		<i>Monjurosuchus</i> sp.	0.5 m				Matsumoto et al., 2007		
Jurassic	Middle	AS-1	Kyrgyzstan	ch-2	Choristodera indet.	?	cr-4	<i>Thalattosuchia</i> indet.	?	
			Balabansai Svita (Calloviaian)				cr-3	<i>Sunosuchus</i> sp.	3 m	Averianov et al., 2006

Table 4.- List of choristoderan localities/horizons with crocodiles in Asia

Tabla 4.- Lista de localidades/horizontes de coristoderos con cocodrilos en Asia.

Leidy, 1852), which is slightly smaller than *Champsosaurus* (*Champsosaurus* 3-4 m; *Thoracosaurus* 2.5 m). However, although the remains of *Thoracosaurus* occur in the same layer as *Champsosaurus*, its bones are much rarer than those of other crocodiles (Pearson *et al.*, 2002), suggesting they may be allochthonous. In support of this, Buscalioni *et al.* (2003) suggested *Thoracosaurus* might be a coastal dweller like other Gavialoidea (including *Eosuchus*, see below), although juveniles may have lived in freshwater environments as in the extant saltwater crocodile, *Crocodylus porosus* (Jouve *et al.*, 2008).

Small incomplete choristoderan jaw elements have been reported from the Oldman and the Dinosaur Park formations of Alberta, Canada, in association with *Champsosaurus* and *Leidyosuchus* (Brinkman, 1990; Gao and Brinkman, 2005; Gao and Fox, 1998) The affinities of these specimens (e.g. UALVP29794; UALVP29795) are uncertain, but the reptiles from which they came, if adult, would have been of similar size to Portuguese (Guimarota) specimens of *Cteniogenys* (e.g. GUI. A.33, Seiffert, 1973).

Paleocene-Eocene

At some Paleocene localities, *Champsosaurus* (~4 m) and *Simoedosaurus* (~5 m) occur together (e.g. Mont-Berru, France, Sigogneau-Russell, 1985, Matsumoto pers. obs. 2008; Fort Union Formation, Wyoming, USA, Bartels, 1983; Ravenscrag Formation, Saskatchewan, Canada, Gao and Fox, 1998). In the Fort Union Formation (Wyoming, Bartels, 1983), these neochoristoderes are recorded with three genera of crocodiles. Of these, the basal eusuchian *Leidyosuchus-Borealosuchus* is similar in size to the choristoderes, but the blunt-snouted alligatorines *Allognathosuchus* and *Ceratosuchus* are smaller. In the Ravenscrag Formation (Russell, 1974) and at Mont Berru (Martin, 2008), *Leidyosuchus-Borealosuchus* again occurs with the neochoristoderes, in conjunction with the large (~4 m) crocodyloid *Asiatosuchus* at Mont Berru (Prasad and Lapparent de Broin, 2002). In each deposit, the crocodiles and choristoderes differ in rostral morphology. By contrast, in the Hannut Formation,

	North America	Europe	Asia
Miocene		EU-9 ch-14 cr-25	
Oligocene		EU-7 ch-13 cr-24	
Eocene			
Paleocene	ch-9 ch-10 NA-9 cr-19 cr-20 cr-21 cr-22	ch-11 EU-6 cr-23	ch-12 AS-8 ?
Cretaceous	Upper ch-7 NA-6 cr-15 cr-16 cr-17	ch-8 EU-4 cr-18	
	Lower ch-5 NA-2 cr-12		AS-7 ch-6 cr-13 cr-14
Jurassic	Upper ch-3 NA-1 cr-5,6 cr-7 cr-8	ch-4 EU-3 cr-9 cr-10 cr-11	
	Middle	ch-1 EU-2 cr-1 cr-2	ch-2 AS-1 cr-3 cr-4

Fig. 6.- Skull morphology of choristoderes and crocodiles in selected horizons, white for choristoderes and black for crocodiles. The horizon numbers (e.g. NA-1) and skull numbers (e.g. ch-1 for choristoderes; cr-1 for crocodiles) correspond to those in Tables 2-4.

Fig. 6.- Morfología del cráneo de los coristoderes y de los cocodrilos en los horizontes seleccionados, en blanco para coristoderes y negro para cocodrilos. Los números en los horizontes (p.ej., NA-1) así como los números en los cráneos (p.ej., ch-1 para coristoderes; cr-1 para cocodrilos) corresponden a los indicados en las Tablas 2-4.

Belgium, *Champsosaurus* co-occurs with the gavialoid crocodile *Eosuchus*, but although they were both recovered from the same shallow marine layer (Sigogneau-Russell and de Heinzelin, 1979), they probably did not live in the same environment. The bones of *Champsosaurus* are rounded, suggesting they were transported into the deposit from upriver, whereas *Eosuchus* may be salt water tolerant (Delfino *et al.*, 2005), as evidenced by the occurrence of the North American species of *Eosuchus* (Marsh, 1870) in marine deposits.

The Paleocene-Eocene Dzhytga 1a and 1b locality, Kazakhstan (Averianov, 2005), is the only Asian locality of this age to yield choristoderes. Crocodiles have

not been recorded but the significance of this is limited, as the faunal assemblage as a whole is depauperate and lacks other freshwater components such as amphibians (Averianov, 2005).

Oligocene-Miocene

The only recorded post-Eocene choristodere is the small European (France, Czech Republic, Germany) *Lazarussuchus* (0.3 m body length, Hecht, 1992). At the Oligocene-Miocene French locality of Armissan, the fauna is poorly known and the presence of crocodiles is uncertain (Hecht, 1992). However, at Oberleichtersbach, Germany (Late Oligocene, Böhme, 2008) and Merkur, Czech

Republic (Lower Miocene, Evans and Klembara 2005), *Lazarussuchus* is found with the much larger (~x7) alligatoroid crocodile *Diplocynodon* (Fejfar and Schelich, 1994).

4. Discussion

4.1 *Choristoderes* within freshwater assemblages

Choristoderes were distributed across Laurasia in the Mesozoic and early Paleogene, typically in relatively warm, temperate climates (occasionally sub-tropical areas, Fig. 5), and in association with a diverse mesic vertebrate assemblage including fish, frogs, salamanders, turtles, and crocodiles (Fig. 4-a). Typically, crocodiles are more diverse than choristoderes (up to 6:1, Fig. 5), although allowance must be made for the fact that many basal crocodiles were predominantly terrestrial. However, there are some well-sampled localities in which either crocodiles (e.g. Lower Cretaceous of China, Japan) or choristoderes (e.g. Lower Cretaceous Purbeck Limestone Group and Wessex Formation, UK) are completely absent. This suggests either differences in habitat preference or some level of competition (whereby choristoderes diversity was limited by the presence of aquatic crocodiles). Generally, the associated freshwater assemblage is similar whether the assemblage contains crocodiles, choristoderes or both, but there does seem to be a tendency for choristoderes to be found in low lying freshwater environments close to coastal margins, at least in the Jurassic, Late Cretaceous and Paleocene (although this may partially reflect the prevalence of this type of deposit). Climate and other physical conditions are likely to have played an important role in choristoderan distribution and possibly extinction (as they do for crocodiles, Markwick, 1998), and this needs to be analyzed more thoroughly than we have space to do here.

Basal, non-neochoristoderan taxa were small and were unlikely to have been in serious competition with the adults of contemporaneous crocodiles, most of which were either larger or occupied a different, more terrestrial, niche. The choristoderes are more likely to have competed for resources with a range of other freshwater animals including predatory fish, turtles, juvenile crocodiles and aquatic lizards, as well as other small choristoderes. Nonetheless, a recent study in central Africa (Luiselli *et al.*, 1999) examined the ecological relationship between the small extant crocodile *Osteolaemus* and a similar-sized potential competitor, the predatory lizard *Varanus*. The two reptiles could co-exist as long as prey was abundant, and this is likely to have been the case for the choristoderes in relation to other small aquatic predators.

With the evolution of the neochoristoderes, there may have been a greater potential for competition with crocodiles, particularly as neosuchian crocodiles were themselves also radiating into more aquatic niches. Neochoristoderes are generally equal, or nearly equal, in size to contemporaneous crocodiles, the only exception being in the Lower Cretaceous Laohongdong Formation of Inner Mongolia, where the neochoristoderes *Ikechosaurus sunailinae* is nearly twice the size of the associated crocodiles. However, this is a special case as contemporaneous East Asian crocodiles mainly belong to basal groups (protosuchians, gobisuchidans and ziphosuchians, Buscalioni *et al.*, 2003) that were primarily terrestrial.

Where several crocodiles, extinct or extant, co-occur they tend to differ morphologically, most notably in rostral shape. Rostral shape in crocodiles is considered to reflect ecology and feeding habits (Busbey, 1994; Brochu, 2001) and it is reasonable to assume the same was true of choristoderes. Busbey (1994) characterised crocodile skulls as platyrostral (dorsoventrally compressed) or oreinirostral (mediolaterally compressed) according to rostrum width/depth indices, and as short, medium or long according to the length of the rostrum relative to overall skull length. However, the same metrics do not work well for choristoderes because their skulls and rostra are more dorsoventrally flattened and because the postorbital skull proportions of crocodiles and choristoderes are very different. Thus plotting choristoderes onto Busbey's (1994) graph of crocodylian skull morphotypes (Fig. 7) fails, for example, to identify neochoristoderes as longirostrine (despite widespread use of the gavial as a functional analogue for *Champsosaurus*: e.g. Erickson, 1972, Evans and Hecht, 1993), and the clearly longirostrine *Simoesosaurus* emerges within the brevirostrine crocodile cluster. Different parameters need to be identified for meaningful comparison. Nonetheless, if crocodiles and choristoderes were interacting ecologically, one would predict that, in any one locality, the choristoderes rostral shape would not be replicated by any of the co-occurring crocodiles. A comparison of rostral shapes (Fig. 6) mainly confirms this prediction, although the comparisons are not statistical. There are two horizons (Upper Cretaceous Hell Creek Formation, Palaeocene Hannut Formation) where crocodiles and choristoderes with slender rostra are found together, but there is reasonable evidence to suggest they did not live together (see above). Indeed, longirostrine crocodylians were primarily in coastal and marine environments, leaving a vacant niche in freshwater ecosystems that neochoristoderes occupied.

In this section, we have focused on the possible ecological relationship between choristoderes and crocodiles because neochoristoderes are most frequently compared

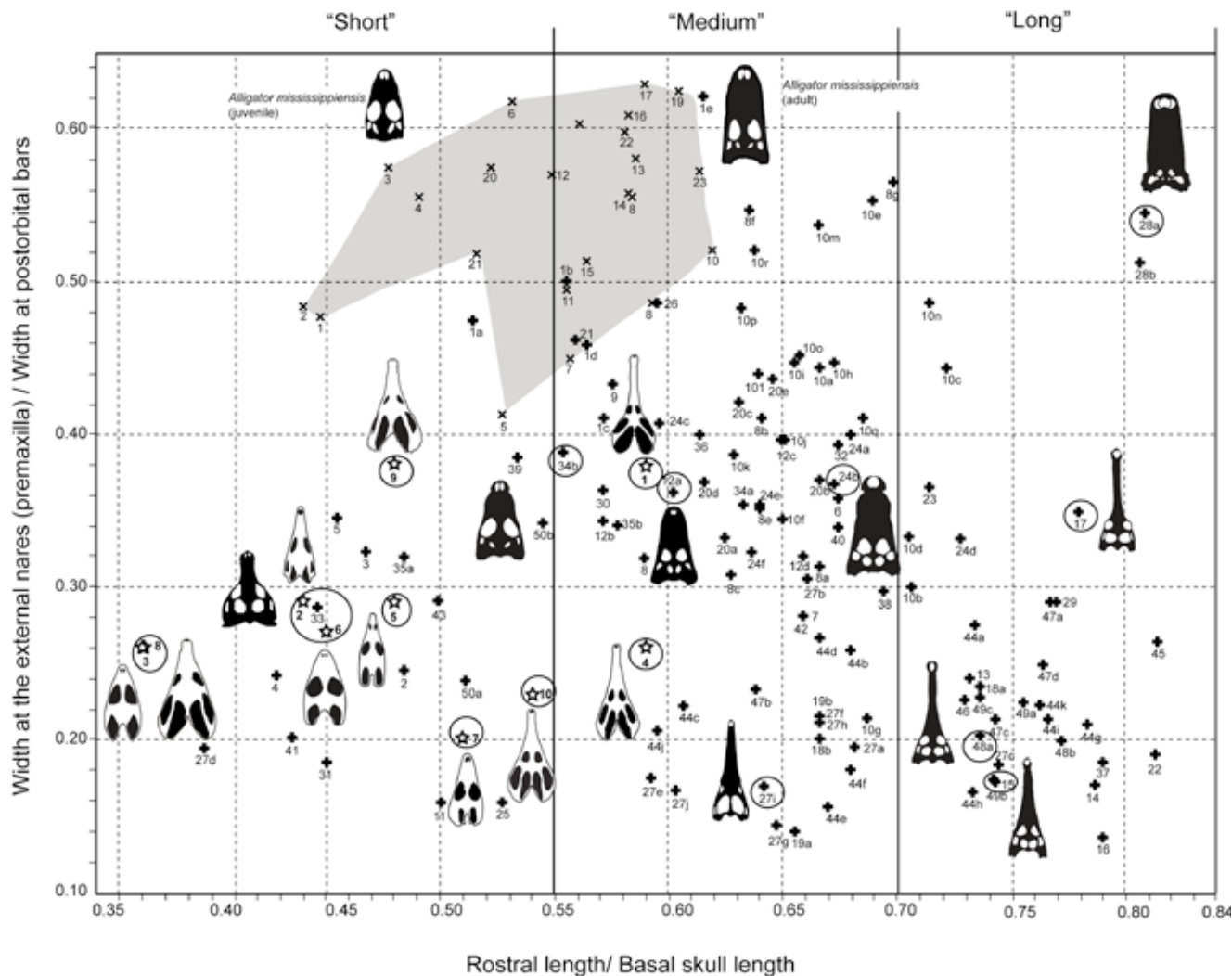


Fig. 7.- Plot comparing rostral width and length for choristoderes and crocodiles (based on Busbey 1994, figure 10. 2). Choristoderes are indicated by numbered stars: 1, *Champsosaurus gigas* (Erickson, 1985); 2, *Cteniogenys* sp. (Evans 1990); 3, *Hyphalosaurus* sp. (IVPP V 14560); 4, *Ikechosaurus pijiagouensis* (Liu, 2004); 5, *Lazarussuchus inexpectatus* (Hecht, 1992); 6, *Philydrosaurus proseilus* (Gao et al., 2007); *Simoedosaurus dakotensis* (Erickson, 1987); *Simoedosaurus* sp. (SMNS 59026); 10, *Tchoiria namsarai* (undescribed Hayashibara specimens). The area marked in grey shows ontogenetic variation for *Alligator mississippiensis*, specimens marked by x. Other crocodiles are marked with crosses. Encircled numbers correspond to illustrated skull silhouettes, choristoderes in white and crocodiles in black silhouettes. The illustrated crocodiles are: 12a, *Diplocynodon darwini*; 15, *Eosuchus lerichei*; 17, *Gavialis lewisi*; 24b, *Leidyosuchus canadensis*; 27i, *Metriorhynchus superciliosum*; 28a, *Mourasuchus amazonensis*; 33 *Orthosuchus stormbergi*; 34b, *Osteolaemus tetraspis*; 48a, *Thoracosaurus macrorhynchus*. For a key to the other crocodiles, see Busbey (1994).

Fig. 7.- Gráfica donde se compara la anchura y longitud rostral en coristoderes y en cocodrilos (basado en Busbey 1994, figure 10. 2). Los coristoderes se indican mediante estrellas numeradas: 1, *Champsosaurus gigas* (Erickson, 1985); 2, *Cteniogenys* sp. (Evans 1990); 3, *Hyphalosaurus* sp. (IVPP V 14560); 4, *Ikechosaurus pijiagouensis* (Liu, 2004); 5, *Lazarussuchus inexpectatus* (Hecht, 1992); 6, *Philydrosaurus proseilus* (Gao et al., 2007); *Simoedosaurus dakotensis* (Erickson, 1987); *Simoedosaurus* sp. (SMNS 59026); 10, *Tchoiria namsarai* (especímenes no descritos de Hayashibara). El área marcada en gris muestra la variación ontogenética de *Alligator mississippiensis*, especímenes marcados con una x. Los demás cocodrilos se han marcado con cruces. Los números incluidos en un círculo corresponden a las siluetas de los cráneos ilustrados (en blanco coristoderes, en negro cocodrilos). Los cocodrilos ilustrados son: 12a, *Diplocynodon darwini*; 15, *Eosuchus lerichei*; 17, *Gavialis lewisi*; 24b, *Leidyosuchus canadensis*; 27i, *Metriorhynchus superciliosum*; 28a, *Mourasuchus amazonensis*; 33 *Orthosuchus stormbergi*; 34b, *Osteolaemus tetraspis*; 48a, *Thoracosaurus macrorhynchus*. La clave para los restantes cocodrilos en Busbey (1994).

with gavialids in terms of lifestyle. However, understanding these potential interactions requires a fuller knowledge of choristoderan diet and lifestyle, which ongoing studies of the gut contents, dentition and skull morphology should help to elaborate.

4.2. Choristoderan evolution and palaeobiogeography

Although the phylogenetic position of choristoderes within Diapsida has yet to be resolved, all of the proposed positions (stem-neodiapsid, basal archosauromorph, sau-

ropterygian relative etc) would predict an origin in the Late Permian or earliest Triassic. As yet, there is no record for that period and thus any discussion of early choristoderan evolution is speculative. Nonetheless, the earliest taxon that can be attributed to the group with confidence is the Middle-Late Jurassic *Cteniogenys* as well as similar, but currently indeterminate material from Central Asia. These early choristoderes are small and constitute part of a freshwater aquatic assemblage that continues almost unchanged (except for the representative genera) until the Miocene. In most cases, these small Jurassic choristoderes are found in swampy or lagoonal freshwater coastal environments. The absence of Permian or Triassic representatives almost certainly reflects the paucity of suitable depositional environments, as evidenced by the absence, or near absence, of Triassic frogs, salamanders, lizards, turtles, and albanerpetontids which typically occur with choristoderes in younger deposits. Choristoderes presumably evolved from small terrestrial-amphibious Permian diapsids within the northern part of Pangea. The Permo-Triassic arid belt may have represented a significant barrier as they did not reach southern Pangea (and have never been recorded from Gondwana).

Small choristoderes had spread across Laurasia by the end of the Jurassic but then disappeared from the Euramerican record (the enigmatic fragments from the Late Cretaceous of Alberta excepted). In Eastern Asia, isolated from the rest of Laurasia in the Middle Jurassic-Lower Cretaceous, the group radiated and diversified, giving rise to the larger neochoristoderes, as represented by *Tchoiria* and *Ikechosaurus*. The apparent absence of aquatic neosuchian crocodiles in these continental localities/ecosystems may well have been crucial to this morphological diversification and almost certainly facilitated the evolution of the large gavial-like choristoderan ecomorphs. In the Lower Cretaceous, Eastern Asia established a connection with western North America, and this may be the route through which neochoristoderes (first recorded in the Barremian of Utah, Britt *et al.*, 2006) entered North America. Neochoristoderes then seem to have established themselves across Laurasia, successfully sharing freshwater ecosystems with eusuchian crocodiles as long as resources were sufficient and there were no direct longirostrine crocodylian competitors. The possible role of crocodiles in the ultimate extinction of neochoristoderes remains unknown, given the accompanying climatic changes at the Paleocene-Eocene transition, but may be clarified with a greater understanding of choristoderan functional anatomy and thus possible areas of niche overlap.

The reappearance of non-neochoristoderes in the Paleogene of Europe was surprising, as reflected by the name

Lazarussuchus (Hecht, 1992). Whether this genus is a relict of the original Jurassic distribution, or was derived from an Asian lineage that reinvaded Euramerica when contact was reestablished, is currently uncertain, as the phylogenetic position of *Lazarussuchus* is not fully resolved (e.g. Matsumoto *et al.*, 2007, 2009; Skutschas, 2008). Material of earlier choristoderes would shed light on this. Finally, although the last record of choristoderes is currently from the lower Miocene, the group may have survived longer at other localities. Albanerpetontid amphibians provide a parallel case. They were long thought to have become extinct in the Miocene (e.g. Estes, 1981) but have since been found in the Lower Pliocene of Hungary (Venczel and Gardner, 2005) and the Late Pliocene of Italy (Delfino and Sala, 2007). A dedicated reexamination of all suitable Mesozoic, Paleogene and Neogene small vertebrate assemblages throughout Laurasia is needed to provide more confident presence/absence data for these periods so that the history, palaeobiogeography, phylogeny, and ecology of this enigmatic reptilian group can be better understood.

5. Conclusions

Choristoderes are generally found in association with a diverse freshwater vertebrate assemblage, in warm temperate environments across Laurasia.

Allowing for preservational and collecting biases, much of the Jurassic choristoderes record, and at least some of that for Late Cretaceous and Paleocene neochoristoderes, comes from low-lying depositional freshwater environments close to the coast. In the Lower Cretaceous of Asia and the Paleogene of Europe, they appear to have been in more continental water bodies.

Choristoderes typically co-occur with crocodiles, but were morphologically most diverse in Asian deposits where aquatic crocodiles were absent.

Neochoristoderes apparently evolved in an isolated Jurassic-Cretaceous Asia, within freshwater environments where the absence (or rarity) of crocodiles left a vacant large longirostrine piscivore niche to be exploited.

Where large neochoristoderes and crocodiles co-occur, the former are typically the only reptiles with strongly longirostrine skulls, suggesting a degree of niche partitioning, aided by the absence of longirostrine crocodiles from Mesozoic and Paleogene freshwater deposits.

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