The fossil vertebrates from Laño (Basque Country, Spain); new evidence on the composition and affinities of the Late Cretaceous continental faunas of Europe

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ABSTRACT

A newly discovered fossil locality at Laño (Basque Country) has yielded a vertebrate assemblage of probably Maastrichtian age comprising fishes, amphibians, reptiles and mammals. It considerably enlarges our knowledge of the Late Cretaceous continental faunas of Europe, hitherto based on a much less complete record. Some taxa are recorded for the first time in Europe, and the fauna also contains the oldest known representatives of some groups (amphisbaenians, salamandrids). The Laño assemblage reveals an original fauna comprising both forms related to Asian and North American groups and elements with Gondwanan affinities.

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INTRODUCTION

Until recently, our knowledge of the Late Cretaceous continental vertebrates of Europe was based on relatively scanty evidence from various localities in Portugal, Spain, France, Austria and Romania (Buffetaut, 1989a). Important new data are provided by the newly discovered Laño locality (Astibia *et al.*, 1987), in the Basque Country, which has been the site of systematic excavations since 1987. The Laño locality differs from other European localities in that it has yielded an abundant and varied assemblage of both large and small vertebrates which gives a much better idea of the real composition of the fauna. This allows more meaningful comparisons with contemporaneous faunas from other continents, leading to important palaeobiogeographical conclusions. We provide here an annotated preliminary list of the Laño vertebrates with special emphasis on their biogeographical significance.

STRATIGRAPHIC POSITION AND DEPOSITIONAL ENVIRONMENTS

The Laño locality is a disused sand quarry near the village of Laño, about 20 km SE of the city of Vitoria (Fig. 1). Geologically, it is located on the southern limb of the Miranda–Treviño synclinorium (central Navarro–Cantabric trough, Basque–Cantabric basin). The core of the structure consists of continental Tertiary strata, with very thick Late Cretaceous sequences to the north and south. The section in the Laño quarry (Astibia *et al.*, 1987) shows a succession of mainly clastic sedimentary units (Fig. 2). The lower unit (S1U3) shows a transition from shallow marine to continental depositional environments. It is separated from the overlying S2U1 unit by a low-angle unconformity; unit S2U1 begins with marine sediments passing upward to continental rocks. Most of the vertebrate remains from Laño have been recovered from sandy and silty levels of the lower subunit of S1U3 (of which a thickness of about 16 m is observable). A detailed sedimentological study of the vertebrate-bearing levels indicates a continental depositional environment affected by high-energy episodes. A braided river system, with channels, inter-channel pools and sandbars, seems to be consonant with the observed sedimentary features. The vertebrate assemblage from Laño is in agreement with a fluviatile environment, as shown, notably by the very large number of fish scales and small crocodilian teeth recovered by sieving; moreover, the dissociated bones found at Laño certainly suggest water transport. One of the most outstanding aspects of this vertebrate-bearing unit

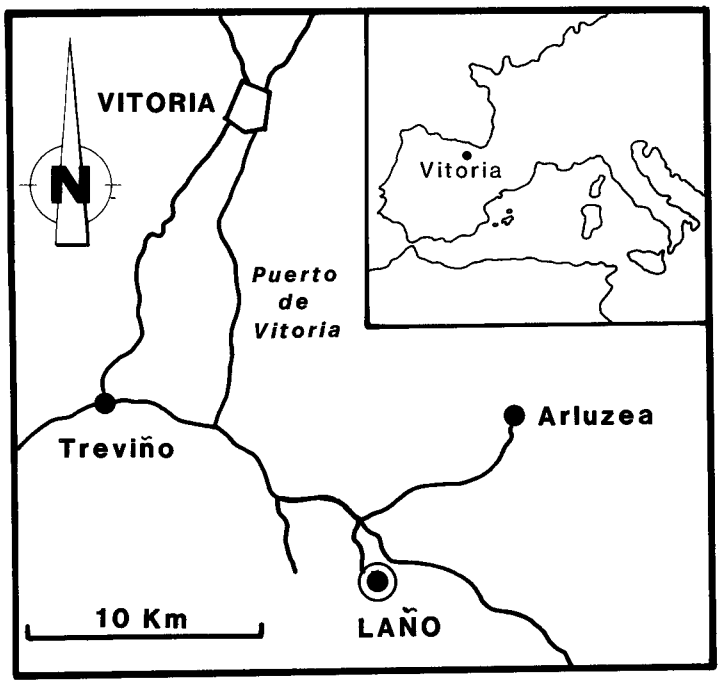

Fig. 1. *Location of the Late Cretaceous Laño locality.*

is the occurrence of ferruginous hardgrounds. The most important bone accumulation is located between two of these hardgrounds. Many of the bones are excellently preserved but often coated and impregnated with iron oxides. The overlying subunit contains shales, sandstones, siltstones and evaporitic layers. The occurrence of black lignitic beds suggests anoxic episodes. A lacustrine environment is likely, with alternating episodes of shallowing and deepening. This subunit has yielded plant remains, poorly preserved bivalves and isolated bone fragments. The base of the unconformably overlying unit S2U1 has a markedly erosive character, with conglomerates, overlain by calcirudites and calcarenites containing orbitoidids, gastropods and shark teeth, together with poorly preserved benthic foraminifers. Unit S2U1 was probably deposited in a littoral shallow marine environment.

The sedimentary features observed at Laño suggest a marked regressive trend, together with a gradual isolation of the sedimentary environments during the Latest Cretaceous. Oscillations from more humid to subaerial episodes may be related to climatic fluctuations.

The microfossils and shark teeth found in unit S2U1 indicate a Maastrichtian age. The exact age of the underlying continental beds with vertebrates is more difficult to assess. To judge from observations at other sections in this area, marine Campanian apparently underlies the sedimentary sequence seen at Laño. This suggests that the Laño vertebrate fauna may be of Early Maastrichtian age.

THE VERTEBRATE ASSEMBLAGE

Palaeontological investigations at Laño have combined the excavation of large specimens with washing and screening of several tonnes of sediment, this site being one of the very few localities in Europe where both large and small vertebrate remains occur together. Every summer since 1987, a group of ten to twenty participants has worked at Laño for one to two weeks. As a result, several thousand bones and teeth, varying in size from less than 1 mm to nearly 1 m, have been recovered. A faunal list is given below, with comments on the more significant taxa.

Class: Chondrichthyes
Order: Lamniformes
Family: Cretoxyrhinidae
Cretolamna appendiculata
Cretolamna sp.

Order: Rajiformes
Family: Sclerorhynchidae
Ganopristis leptodon

Order: Myliobatiformes
Family: Rhombodontidae
Rhombodus binkhorsti

All the above-mentioned sharks and rays, represented by teeth, come from the marine upper unit S2U1. *Rhombodus binkhorsti* is known only from the Maastrichtian (Cappetta, 1987) and thus provides an important indication about the age of this unit.

Class: Osteichthyes
Order: Lepisosteiformes
Family: Lepisosteidae
Lepisosteus sp.

Class: Amphibia
Order: Anura
Family: Discoglossidae

Two sacral vertebrae and several dorsal vertebrae belong to discoglossid frogs. The family has marked 'Laurasian' affinities and is known since the Early Cretaceous (Estes and Sanchiz, 1982).

Family: Palaeobatrachidae

Order: Caudata
Family: Prosirenidae
cf. *Albanerpeton* sp.

Two distinctive elements indicate the occurrence of this taxon: a tiny dentary fragment and the distal half of a humerus. These specimens are the smallest known representative of this taxon; those from the Early Cretaceous of Galve (Spain) (Estes and Sanchiz, 1982) are about 50% larger.

Family: Salamandridae
Genus and species indet.

Three tiny vertebrae (centrum length 1 mm or less) indicate the presence of this family without much doubt. The rectangular neural arches suggest that

these specimens may be related to *Salamandra*, although poor preservation makes any suggestions of generic affinities doubtful. This is the earliest record of a salamandrid (the previous earliest record was from the Middle Eocene of Europe).

Class: Reptilia
Order: Testudinata
Family: Dermatemyididae

Represented by abundant vermiculated plates and partial shells.

Order: Sauria
Infraorder: Scincomorpha
Genus and species A

The general appearance of a dentary fragment with one relatively complete cylindrical tooth suggests that it is a scincomorph; the robust and well-defined sub-dental gutter is more like that of a scincomorph than like that of an iguanian.

Genus and species B

A tiny dentary fragment (about 2 mm in length) bears two distinctive teeth, with expanded tricuspid crowns and relatively short tooth bases. In general appearance these teeth are reminiscent of those of some iguanine iguanians, but the specimen is too incomplete to warrant identification at the family level. A few scincomorphs have tricuspid (but unexpanded) teeth; expanded, tricuspid teeth may occur among teiids but generally are of different shape. Among scincids and cordylids, a few taxa have teeth of this sort, but it is a rare condition.

Order: Serpentes
Family: Madtsoiidae
Madtsoia sp.

A complete vertebra (Fig. 3) and several fragmentary ones show the typical features (especially the parazygantral foramina) of madtsoiid snakes. They are clearly referrable to the genus *Madtsoia*, but some characters indicate a new species. This is the first record of a madtsoiid snake in a Laurasian area. Madtsoiid snakes have previously been recorded from the Senonian of Niger, the Campanian of Madagascar, the Palaeocene of Morocco, the Late Cretaceous, Palaeocene and Eocene of Argentina, the Palaeocene of Brazil and

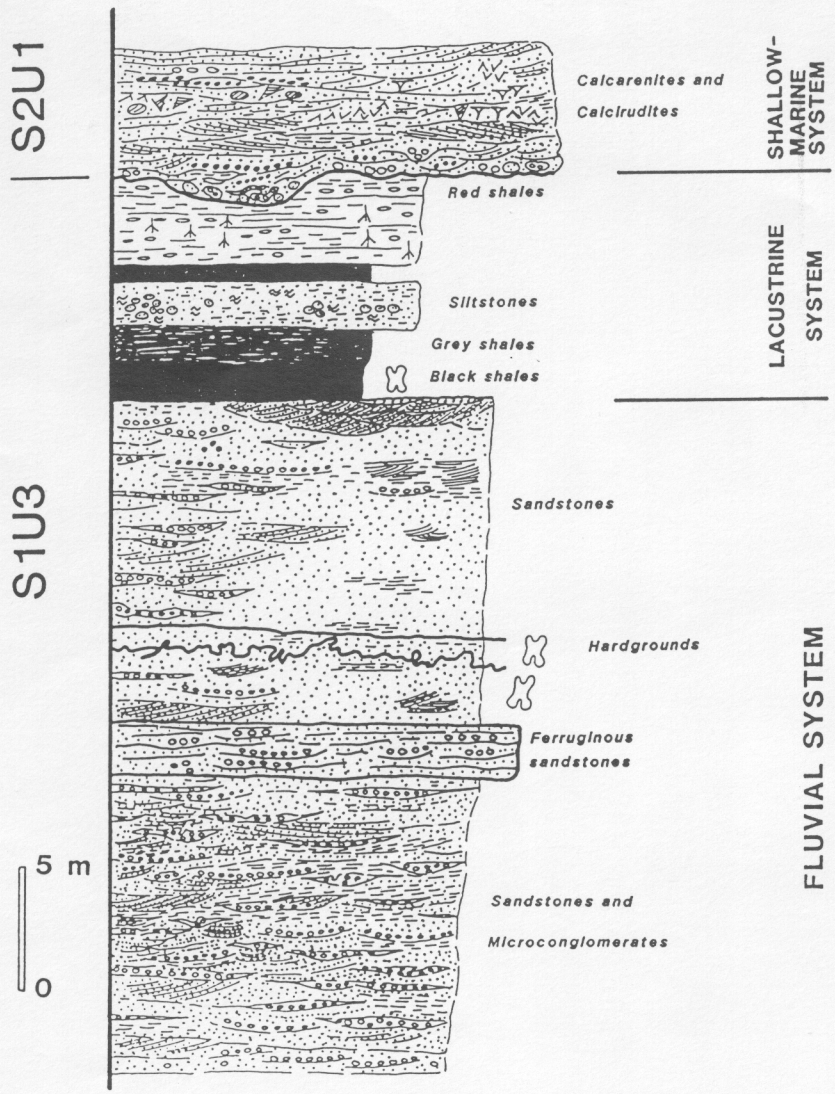

Fig. 2. *Stratigraphic section at Laño quarry. Symbols on the right side of the log identify the main vertebrate-bearing horizons.*

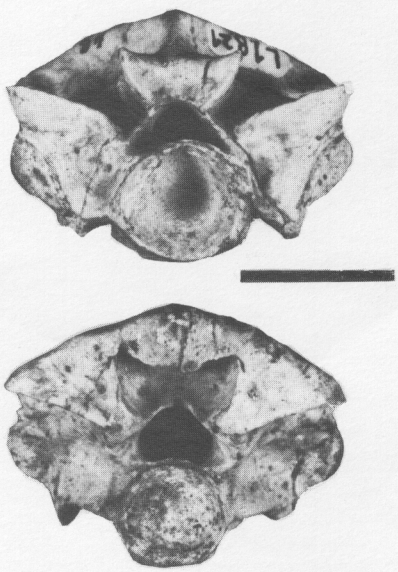

Fig. 3. *Vertebra of the 'Gondwanan' snake Madtsoia in anterior* (a) *and posterior* (b) *views. Scale bar: 1 cm. Photographs by I. Gaztambide.*

the Pleistocene of Australia (Rage, 1987).

Family: Aniliidae

Several small vertebrae constitute the first record of an aniliid snake in the Cretaceous of Europe. In the Cretaceous, this family was previously known only from North and South America.

Order: Amphisbaenia
Family: indet.

Five procoelous vertebrae show a dorsoventrally compressed cotyle and condyle, and lack a neural spine and a hemal keel. They may belong to an amphisbaenian, in which case this would be the oldest record of this group (the oldest record was hitherto from the Palaeocene of North America).

Order: Crocodylia
Suborder: Mesosuchia
Family: Trematochampsidae?

A small amphicoelous dorsal vertebra and a few blunt teeth with wrinkled enamel and irregularly serrated carinae may belong to a mesosuchian crocodilian of the family Trematochampsidae. This is a predominantly Gondwanan family, known from the Cretaceous of Africa, South America and Madagascar, but it has also been reported from the Upper Cretaceous and Eocene of Europe (Buffetaut, 1989a).

Suborder: Eusuchia
Family: Alligatoridae?

The occurrence of an alligatorid-like crocodilian with crushing posterior teeth is documented by very numerous button-like teeth and several jaw fragments. Such forms are widespread in the Upper Cretaceous of North America and have also been reported from Late Cretaceous localities in Europe (Buffetaut, 1980).

Family: Crocodylidae

A crocodylid with slender festooned jaws and pointed teeth is represented by jaw material (including a very well-preserved lower jaw) and isolated teeth. It may be referrable to the genus *Allodaposuchus*, from the Upper Cretaceous of Transylvania and France (Buffetaut, 1980).

Order: Saurischia
Suborder: Theropda
Family: Abelisauridae?

A badly crushed right femur and the proximal end of a left femur show an unusually narrow neck, very different from most of the well-known Cretaceous theropods of Laurasia, but reminiscent of the Abelisauridae. The Abelisauridae are a group of large theropods known mainly from the Cretaceous of the southern continents (South America, India; see Bonaparte and Novas, 1985; Bonaparte and Kielan-Jaworowska, 1987); an abelisaurid has already been reported, on the basis of a maxilla, from the Maastrichtian of southern France (Buffetaut, Mechin and Mechin-Salessy, 1988), and a femur very similar to those from Laño has been found in the Campanian of Provence.

Theropoda indet.

The Laño locality has yielded about fifty small isolated theropod teeth. They are compressed and serrated, and at least two types can be distinguished among them, one with serrations on the posterior edge only and one with serrations on both edges. This suggests the occurrence of at least two distinct theropods. The small size of the teeth indicates either juveniles of large species (indicated by a few large teeth, 3–5 cm long) or fully grown small theropods. The large teeth at least may belong to the same form as the above-mentioned femora.

Suborder: Sauropoda
Family: Titanosauridae

Most of the dinosaur remains found at Laño belong to titanosaurid sauropods. They include both tiny isolated cigar-shaped teeth a few millimetres long, which probably belonged to 'baby' titanosaurids, and teeth (Sanz, 1986), vertebrae and limb bones of adults. The caudal vertebrae are typically procoelous. Another autapomorphic titanosaurid feature found on the Laño specimens is the cellular bony structure of the vertebrae. Titanosaurids are a mainly Gondwanan group, with one genus (*Alamosaurus*) from the Upper Cretaceous of southern North America often considered as a South American immigrant (Bonaparte, 1984; Lucas and Hunt, 1989). They are abundant in many late Cretaceous European localities, however, and may have been present in Europe since the Early Cretaceous (Buffetaut, 1989b). Titanosaurids are by far the dominant herbivorous dinosaurs at Laño. This dominance of titanosaurids is rather common on the southern continents, as well as in at least some localities in the Maastrichtian of southern France (Buffetaut *et al.*, 1989).

Order: Ornithischia
Family: Hypsilophodontidae
Rhabdodon priscus

A single complete tooth belongs to the hypsilophodontid *Rhabdodon priscus*. Ornithopod dinosaurs are thus very rare at Laño, where no hadrosaur remains have been found.

Family: Nodosauridae
Nodosauridae indet.

Fragmentary remains of a small ankylosaur (2–3 m long) have been found at Laño, including an incomplete left dentary (Fig. 4), a maxilla fragment, small isolated teeth, one ulna, rib fragments, and scutes. A preliminary study of the dentary reveals conservative nodosaurid features (such as a long tooth row and a relatively high coronoid process). Comparison with the only other ankylosaur lower jaw available from the Upper Cretaceous of Europe (from the Campanian Gosau beds of Austria; Seeley, 1881) reveals morphological differences which suggest that the Laño ankylosaur may belong to a new taxon.

Order: Pterosauria
Family: Azhdarchidae

Pterosaurs are represented at Laño by a number of fairly well preserved vertebral and limb elements. A fourth

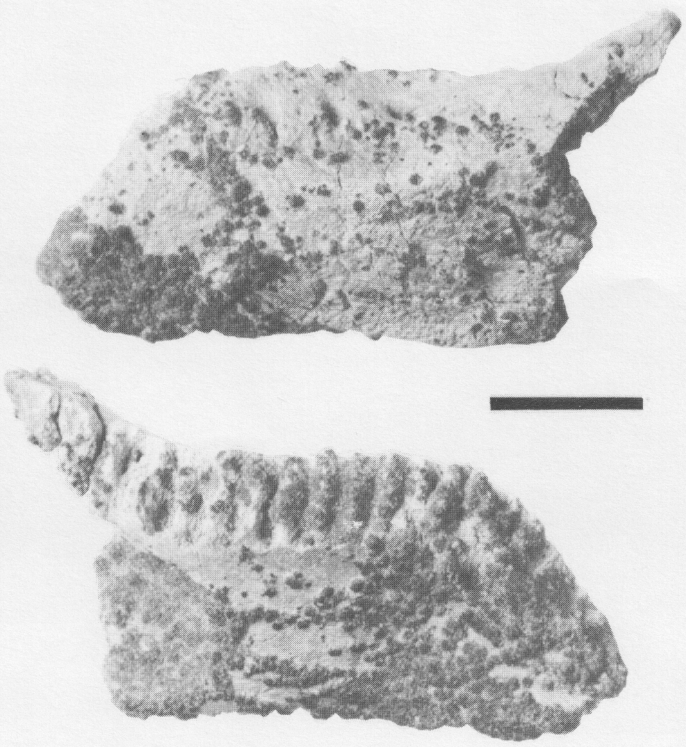

Fig. 4. *Left dentary of a small nodosaurid ankylosaur in lateral* (a) *and medial* (b) *views. Scale bar: 2 cm. Photographs by C. Abrial.*

Fig. 5. *Notarium of an azhdarchid pterosaur in right lateral view. Scale bar: 2 cm. Photograph by C. Abrial.*

metacarpal and several phalanges of the fourth finger indicate a wing span of several metres. The vertebral column is represented by a large notarium (Fig. 5) and elongated cervical vertebrae. The notable elongation of the cervical vertebrae allows to refer the Laño pterosaur to the family Azhdarchidae. Azhdarchids are large to gigantic pterosaurs (Nesov, 1984; Bennett, 1989) which had a very wide geographical distribution in the Late Cretaceous. Although pterosaur remains have been reported from the Upper Cretaceous of Portugal and Transylvania, none of this material has been properly described and the Laño specimens are by far the best Late Cretaceous pterosaur remains hitherto found in Europe.

Fig. 6. *Left lower molariform tooth of indeterminate therian (marsupial ?) in occlusal view. Scale bar: 0.5 mm. Photograph by C. Abrial.*

Class: Mammalia
Theria indet. A (Marsupialia?)

The best mammal tooth hitherto found at Laño (Fig. 6) is a small left lower molariform tooth (length: 1.75 mm; width: 1.05 mm). The metaconid and talonid are deeply worn and the hypoconulid is broken, which makes it difficult to place it with any precision. The roots are lacking. The trigonid is much elongated. The very anterior paraconid is low and labial to the metaconid. The latter is posterior to the protoconid, which is rather low although it is the highest cuspid of the talonid, the paraconid being the lowest one. The talonid basin is deeply worn. The hypoconulid and entoconid seem rather close to each other, but their exact relationships cannot be observed with any accuracy. Several characters (thin enamel, general shape of the tooth, relationships of paraconid and metaconid) are those of a decidual tooth. The exact affinities of this tooth are unclear, mainly because of the damaged hypoconulid. However, Late Cretaceous eutherians usually show a clearly central hypoconulid (Clemens and Lillegraven, 1986), which is definitely not the condition observed in the Laño tooth. In Late Cretaceous marsupials, great variation of the relative position of the entoconid and hypoconulid may occur within a single species. This tooth may belong to a marsupial, but it differs from all marsupial teeth hitherto described. Additional material is needed

to better define the affinities of this form.

Theria indet. B

A lower left molar shows very peculiar features. The talonid basin is much worn and the hypoconulid is broken. The trigonid is relatively low, with very worn broad and bulbous cuspids. The protoconid is the highest cuspid, whereas the paraconid is very low and labial to the metaconid. In front of the protoconid, a broad cingulum bears a wear facet. The talonid basin is wide and elongated. The hypoconulid and entoconid are twinned on a promontory. This is a marsupial character, but most other characters (bulbous cuspids, broad cingulum) are not reminiscent of any known marsupial. However, it should be remembered that our knowledge of Late Cretaceous marsupials outside North America is very poor.

CONCLUSIONS

The Laño assemblage considerably increases our knowledge of the Late Cretaceous vertebrate faunas of Europe. It includes the oldest records of two groups (amphisbaenians, salamandrids), as well as the first European records of one other (madtsoiid snakes). Although the systematic relationships of the mammal teeth so far found at Laño are problematical, these specimens are important in the European context: the Late Cretaceous mammals of Europe were hitherto known only from a few specimens from three sites in Portugal (Antunes *et al.*, 1986), southern France (Ledoux *et al.*, 1966) and Transylvania (Grigorescu *et al.*, 1985). The Laño assemblage provides important indications concerning the biogeographical affinities of Late Cretaceous European vertebrates. Although some groups present at Laño, such as the salamandrids, discoglossids and palaeobatrachids, have an essentially Laurasian distribution, several others (madtsoiids, trematochampsids, abelisaurids, titanosaurids) indicate close links with the southern continents. The Laño megafauna, dominated by titanosaurid and abelisaurid dinosaurs, with ornithischians playing a much less important part than in contemporaneous North American or Asian faunas, is clearly reminiscent of the South American, Indian or African assemblages of the Late Cretaceous. This indicates that Late Cretaceous Europe (or at least its Franco-Iberian part) had closer faunal links with the southern continents than with either western North America or mainland Asia, which suggests interchange between Europe and Africa sometime during the Cretaceous (as already suggested by Bonaparte, 1986, and Buffetaut, 1989a). As far as continental vertebrate faunas are concerned, the latest Cretaceous world was much more diverse than it was thought a few years ago. This should be taken into consideration when discussing scenarios of terminal Cretaceous mass extinctions.

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