# Taphonomy of the Late Cretaceous dinosaur-bearing beds of the Laño Quarry (Iberian Peninsula)

X. Pereda-Suberbiola [a,b,*], H. Astibia [a], X. Murelaga [a], J.J. Elorza [c],
J.J. Gómez-Alday [c]

[a] *Universidad del País Vasco/Euskal Herriko Unibertsitatea, Zientzi Fakultatea, Paleontologia eta Estratigrafia Saila, Postakutxa 644, 48080 Bilbao, Spain*
[b] *Muséum National d'Histoire Naturelle, Laboratoire de Paléontologie, 8 rue Buffon, 75005 Paris, France*
[c] *Universidad del País Vasco/Euskal Herriko Unibertsitatea, Facultad de Ciencias, Departamento de Mineralogía y Petrología, Apartado 644, 48080 Bilbao, Spain*

## Abstract

The Laño quarry, located in the northern part of the Iberian Peninsula (Basque–Cantabrian Region), has yielded a diverse continental vertebrate assemblage from the Late Cretaceous (late Campanian to early Maastrichtian). The fossil assemblage consists of almost 40 species, including bony fish, amphibians, lizards, snakes, turtles, crocodilians, dinosaurs, pterosaurs and mammals. Laño is the most productive European vertebrate locality hitherto known from the Late Cretaceous. The sedimentology of the Laño section shows that the three associated fossiliferous beds (known as L1A, L1B and L2) were deposited in an alluvial system composed primarily of fluvial sands and silts. The sedimentary structures are consistent with channel areas within an extensive braided river. The L1A level was excavated in detail and mapped following a square-metre grid system. The main features of the multispecies vertebrate assemblage are as follows: wide range of body size (including microfossils); large proportion of adult individuals; rare articulated skeletal parts; size-sorting and dominance of small elements; high spatial density; long bones showing some preferential orientation; variable dip; variable degree of breakage and large proportion of splintering; wide range of weathering and abrasion; no evidence of predatory activity or chemical alteration. On the basis of these features, we suggest that the Laño association lies between the taphonomic modes for attritional vertebrate assemblages in fluvial channels, though it tends more toward the channel-fill than the channel lag mode. The L1A sample of Laño is a heterogeneous assemblage of elements ranging from isolated bones and teeth to articulated skeletons with allochthonous and para-autochthonous characteristics. It consists of a mixture of vertebrates from different palaeocommunities, and includes aquatic (or semi-aquatic) elements and remains transported from a variety of habitats on the alluvial plain. The dinosaur bones are commonly broken and show a greater degree of abrasion than those of freshwater vertebrates, indicating that they may be allochthonous. However, actinopterygians, amphibians, pleurodiran turtles and eusuchian crocodilians are interpreted as being para-autochthonous. Palaeobatrachid frogs, bothremydid turtles and alligatoroid crocodilians are the most relatively abundant vertebrates of the Laño fossil assemblage. The occurrence of pelomedusid turtles and crocodilians is indicative of an intertropical, warm climate. © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:* Iberian Peninsula; Late Cretaceous; palaeoecology; taphonomy; vertebrates

---

\* Corresponding author. Tel.: +34-94-601-26-30; fax: +34-94-464-85-00.
*E-mail address:* gpbmubej@lg.ehu.es (X. Pereda-Suberbiola)

## 1. Introduction

Taphonomic studies of continental vertebrate fossil assemblages provide interesting information for the interpretation of palaeoenvironments (Efremov, 1940; Voorhies, 1969; Behrensmeyer and Hill, 1980; Behrensmeyer, 1991; Lyman, 1994; Fiorillo, 1997). Most research on the vertebrate record has been focused on Tertiary mammal assemblages. However, only limited research has been done on Mesozoic sites. Moreover, nearly all the taphonomic analyses of Late Cretaceous assemblages are based on the well-known western sites in North America (e.g. Dodson, 1971; Dodson et al., 1980; Lucas, 1981; Rogers, 1990; Fiorillo, 1991; Varricchio, 1995). In Europe, detailed vertebrate taphonomic works deal with Tertiary and Quaternary mammals (Belinchón, 1987; Noe-Nygaard, 1987; Schwarcz et al., 1989; Alcalá Martínez, 1994; Montoya, 1994), while only a few studies have been carried out on Mesozoic dinosaur-bearing assemblages (e.g. Grigorescu, 1983). We present the results of a taphonomic study based on an Upper Cretaceous section in the Iberian Peninsula, which has yielded a very rich and diversified continental vertebrate fauna, consisting mainly of reptiles (Astibia et al., 1987, 1990a).

The main purpose of this paper is to review taphonomic features of the continental vertebrate assemblage at the Laño quarry and to interpret the taphonomic history of the fossil association. The taphonomic analysis involves the study of a large number of variables within a well-defined sedimentological context. Preliminary taphonomic data have already been published by Pereda-Suberbiola et al. (1992).

## 2. Geological setting

The Laño site is an abandoned sand quarry within the Condado de Treviño, about 25 km south of the city of Vitoria-Gasteiz, in the Province of Alava (Fig. 1). Geologically, the Laño quarry is located on the southern part of the Sud-Cantabrian Synclinorium, a large structure mainly composed of Upper Cretaceous and Tertiary deposits, which stretch for more than 100 km from east to west, in the Basque–Cantabrian Region (Astibia et al., 1987; Baceta, 1996).

The section in the Laño quarry shows several low-angle unconformities related to the synsedimentary activity of the adjacent Peñacerrada diapir. Approximately 85% of the stratigraphic record at the Laño site represents upper
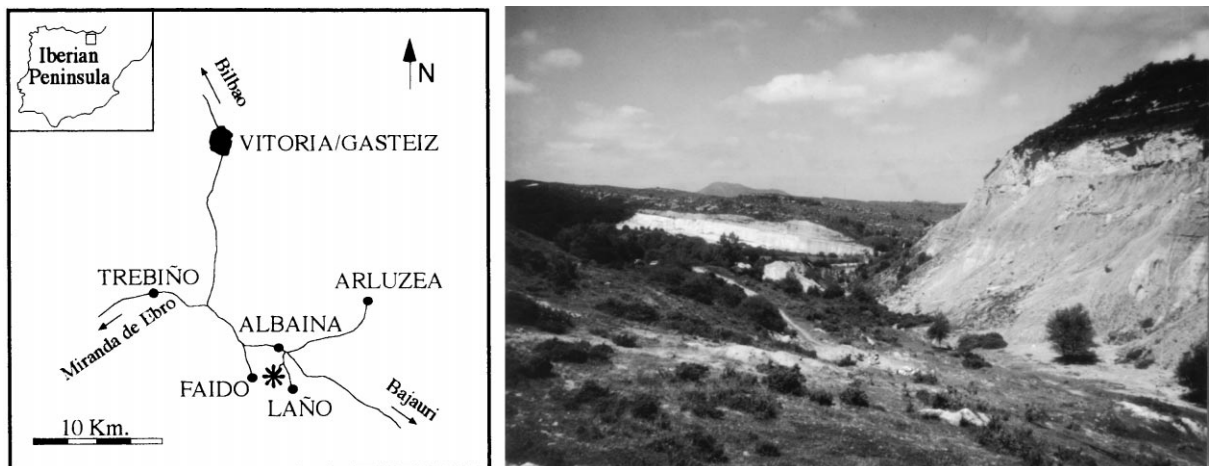


Fig. 1. Geographical location and general view of the Laño quarry (Iberian Peninsula). The deposits of the foreground corresponds to the Laño section (the two main vertebrate levels outcrop in the center of the photograph), and the white beds on the middle ground correspond to the Albaina section.

Campanian–lower Maastrichtian continental deposits. Most of the vertebrate remains have been recovered from siliciclastic bedload deposits (Astibia et al., 1987, 1990a; Gómez-Alday et al., 1994; Gómez-Alday and Elorza, 1998). The upper part of the section shows upper Maastrichtian coastal deposits that have yielded a diverse marine fauna (Bardet et al., 1997). The most important regional discontinuity is an intra-Maastrichtian unconformity (Baceta, 1996) (Fig. 2).

The continental vertebrate-bearing unit of the Laño quarry has been provisionally correlated with the upper Maastrichtian Sobrepeña Formation of the Burgos Province by Floquet (1991). Nevertheless, Baceta (1996) regarded the Laño continental beds as roughly equivalent to marine sediments of the upper part of the Vitoria Formation (Alava Province). Based on this geological evidence, the most likely age of the continental vertebrate fauna of Laño is late Campanian or, less likely, early Maastrichtian.

## 2.1. Lithofacies and depositional environments

Taphonomic analyses commonly involve the study of associated lithofacies. The section in the Laño quarry shows a succession of mainly clastic sedimentary rocks, including both continental and marine deposits (Gómez-Alday et al., 1994). In the 115 m thick largely terrigenous succession of the study area, from the Laño quarry in the west to the Bajauri road in the east, five major depositional systems are recognized from the base to the top (Fig. 2): (1) lower alluvial systems, which comprise: (a) fluvial sands and conglomerates with disc-shaped clasts; (b) fluvial mudstones and sands; and (c) fluvial sands and conglomerates with subspherical clasts; (2) lower palustrine systems; (3) upper alluvial systems; (4) upper palustrine systems; and (5) coastal systems.

A 65 m thick siliciclastic succession is well exposed in the Laño quarry (Fig. 3); all the above-mentioned depositional systems are not repre-
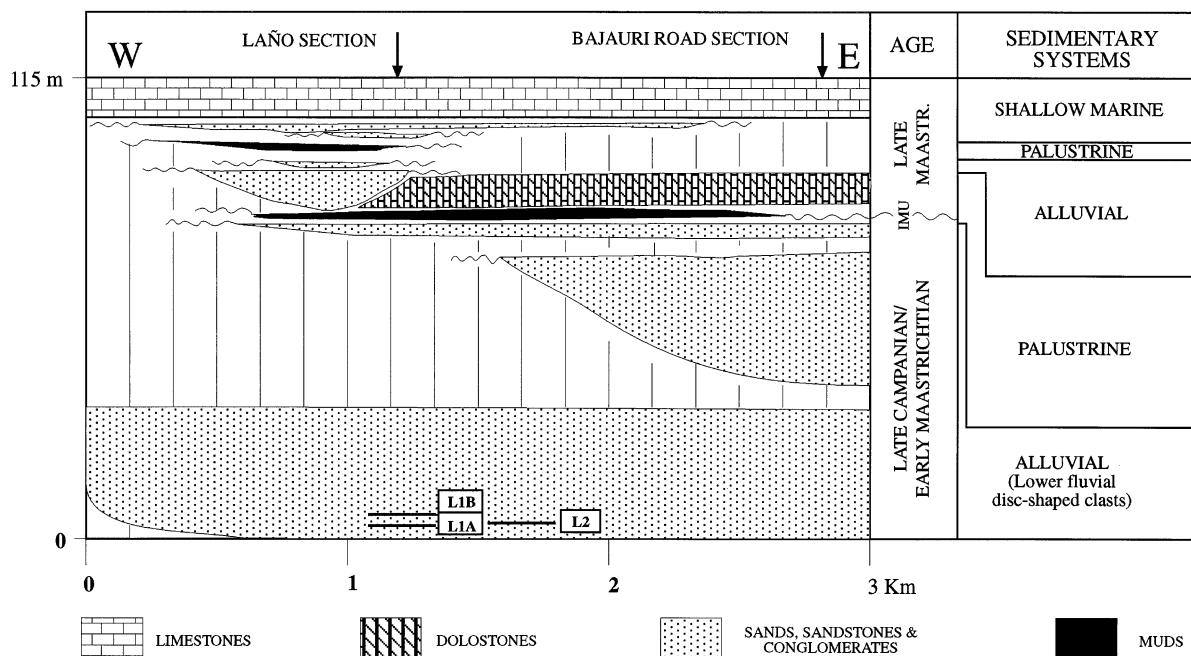


Fig. 2. Schematic W–E general stratigraphic section of the Laño quarry and Bajauri road sites showing the different depositional systems and major unconformities during the Late Cretaceous. Vertical lines do not show an accurate time of no sedimentation. L1A, L1B and L2 are the main vertebrate fossil-bearing levels. Wavy lines represent unconformities. IMU is an intra-Maastrichtian unconformity of regional importance (see Baceta, 1996).
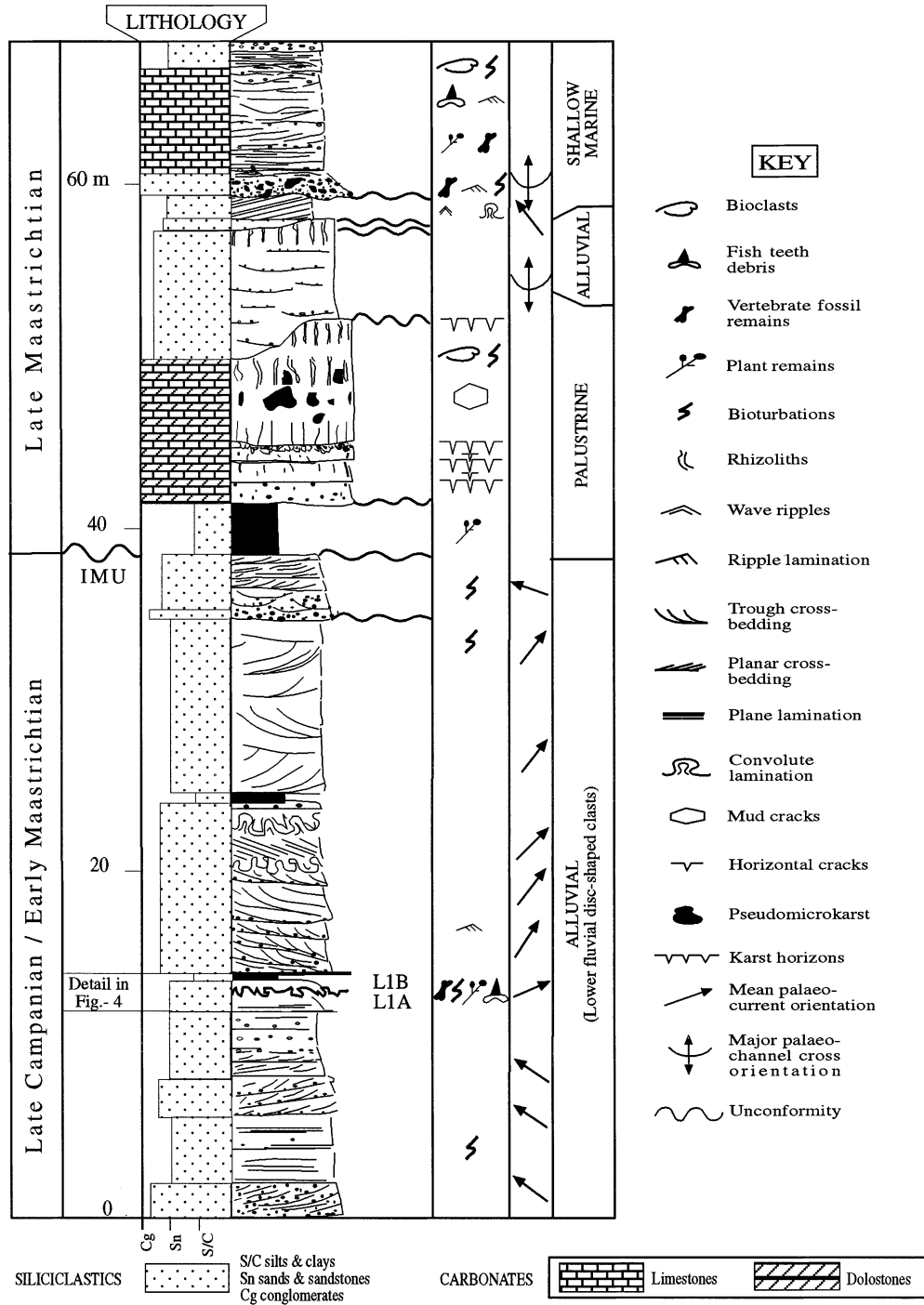
Fig. 3. Stratigraphic–sedimentological section and location of two of the vertebrate fossil-bearing beds (L1A and L1B levels) at the Laño quarry site.

sented due to erosional features related to the synsedimentary diapiric activity. Most of the continental vertebrate remains occur in fluvial sands with disc-shaped clasts of the lower alluvial system. This unit comprises hard to poorly consolidated sandy conglomerate beds whose boundaries are parallel surfaces that delimit tabular-shaped bodies; at the base, they show low relief scoured surfaces, with a lateral extension of up to 2 km. The internal organization mostly involves through and planar cross-bedding that is interpreted as representing transverse bars with variable orientation. The accretion of composite forms in the channel areas gives tabular sets of cross-bedding of different scales, types and orientation, suggesting larger sand flats. The appearance of internal erosional surfaces suggests that bedforms were modified during repeated high-flow–low-flow alternating stages. The interchannel areas are not well represented although they have a lateral conti-

nuity of several hundred metres. They comprise fining-upward deposits characterized by gravels and blackish to reddish mudstones, 0.2–1 m thick. They are interpreted as overbank deposits infilling shallow ephemeral ponds.

The bone-associated deposits, about 2 m thick, have been studied in detail in two stratigraphic sections at the Laño quarry (Fig. 4). The so-called Albaina section is located in the occidental part of the quarry and the Laño section in the area (central and oriental part of the quarry) where most of the vertebrate remains have been recovered. The Albaina section begins with a gravel lag composed of siliceous clasts (the largest is about 7 cm long), and 1 m thick, trough cross-bedding conglomeratic sands up to trough cross-laminated, moderate to fine-grained sands. The sandy beds pass upward to about 50 cm thick siliceous, 0.8 cm grained, conglomerates with sandy matrix, 60 cm moderate to fine-grained sands showing trough cross-bed-
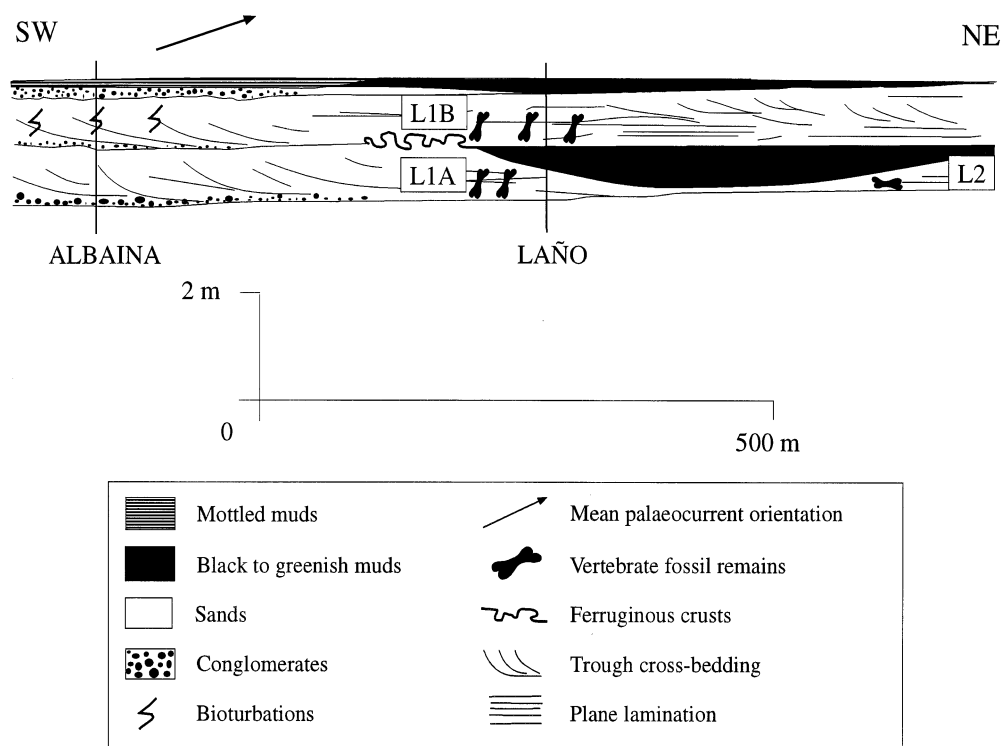


Fig. 4. Channel cross-section from SW to NE of the Laño quarry. The L2 level is interpreted as a lateral equivalent of the L1A level; L1B overlies the L1A level.

ding. Bioturbations have been observed at the top of this bed. The whole succession is interpreted as channel deposits. The Albaina section ends showing upwards a scoured surface of low relief, followed by 10 cm thick apparently massive conglomerates and, finally, 20 cm thick, pink–violet–white mottled mudstones. The youngest beds are interpreted as splay deposits.

One of the most outstanding aspects of the vertebrate-bearing beds is the occurrence of ferruginous crusts. The most important bone accumulations are associated with two of these crusts (Elorza et al., 1999). The section displays, from bottom to top, the following succession of sedimentary structures: L1A sands and laminated sands, with vertebrate remains, that pass upward to laminated muds with plant remains, up to an irregular ferruginous surface; L1B level including sands of low flow regime and upward greenish to blackish sandy mudstones. L1B ends with a fairly regular and thick ferruginous surface. The L2 level, which outcrops in the northeastern part of the quarry, is considered as a lateral equivalent of the L1A level (Fig. 4).

The sedimentary features suggest that the L1B level is more energetic than the underlying L1A. The L1B level is mainly composed of sands and has yielded a greater number of large bones at Laño, whereas the L1A level consists of mud and sand deposits and both micro- and macrofossils occur together. L2 facies are mainly composed of fine- to medium-grained deposits such as sands and greenish muds, which contain both small and large bones.

The listed lithological differences suggest two distinct positions within the same palaeochannel, which was probably covered by crevasse splay deposits. The central and more active areas are located towards the west, whereas in the east, fine-grained sediments (settling area) are dominant.

Palaeocurrents measured in the larger bedforms show downflow discharges towards the north-east. A braided-type fluvial system developed in a wide alluvial plain several kilometres wide seems to be consonant with the sedimentological features.

The regional palaeogeography and palaeocurrent data suggest that the coast line was situated towards the north.

## 3. Methods

The presence of fossil vertebrates in Laño has been known since 1984 when the palaeontologist Xabier Orue-Etxebarria discovered dinosaur remains in the quarry. Subsequent collections were made by members of the Universidad del País Vasco/Euskal Herriko Unibertsitatea (UPV/EUH, Bilbao) during 1985 and 1986. Since then, a detailed investigation of the continental units has been carried out in collaboration with the Universidad Autónoma de Madrid (UAM), the Centre National de la Recherche Scientifique (CNRS, Paris), the Université Pierre et Marie Curie (Paris VI), the Université de Montpellier II and the Museo de Ciencias Naturales de Alava/Arabako Natur Zientzien Museoa (MCNA, Vitoria-Gasteiz). The macrofossils were collected by detailed surface-digging at three main levels, called L1A, L1B and L2. The estimated total volume of sediment removed during the field work is more than 50 m$^3$. During the 1995 field season, a detailed map of L1A was made to study the distribution of bones in the quarry. In addition, sediment from the L1A level was screenwashed to obtain microfossils. About 8 tonnes of silty and sandy sediments were washed by our team and, as result, about 25 kg of residue were obtained.

### 3.1. Field work

During the 1995 field season, the L1A level was excavated in detail and mapped following a metre-square grid system. Only remains larger than 1 cm (but also identifiable fossils such as teeth and ganoid scales) were taken into account. About 4–5 m$^3$ of sediment were removed during the excavation, which represents a surface approximately 5 m wide by 2 m long; in some areas, a depth of about 50 cm was reached. As a result, more than a thousand fossils were recorded, and most of them were collected (see Section 3.4 method biases). The bone accumulation of the L1A level was carefully drafted in field maps to record the relative location of all the specimens.

Prior to the excavation, a mechanical shovel was used to remove the overburden. The beds were dug using a conventional set of tools, e.g. picks,

spades, shovels, brushes, and knives. The equipment needed to prepare a grid for field mapping included large nails, that were used as tie points, and a stretched band between points to define individual cells. Moreover, a small-scale wooden grid was employed to plot the location of the large bones.

The microfossils have been studied separately as they could have had a different taphonomic history. The microfossils were obtained by screen-washing of sandy mudstones from the L1A level. Two meshes were used during screen-washing, with wire openings of 2 and 0.7 mm, respectively. About 3 kg of concentrated residue were obtained from each tonne of washed sediment.

### 3.2. Laboratory phase

The laboratory phase of this work involved preparation and restoration of the macrofossils using standard methods. These methods included both mechanical and chemical techniques. The Laño specimens were prepared in the Laboratory of Palaeontology of the UPV/EHU (Bilbao) and in the Department of Geology of the MCNA (Vitoria-Gasteiz). The field record data supplemented observations made in the laboratory. The microfossils were extracted by hand-picking under the binocular microscope.

The taphonomic methods employed here follow Behrensmeyer (1991). We have calculated the index described in the literature to express the ecological diversity (see Magurran, 1988). The body weight of the Laño vertebrates was estimated following Anderson et al. (1985) for dinosaurs and Damuth and MacFadden (1990) for mammals. Moreover, comparisons with living forms were made where applicable. The size categories and the articulation states are those described by Behrensmeyer (1991), and the size distribution is that of Goldstein (1981). Skeletal element representation was recorded as Voorhies Groups (Voorhies, 1969), as well as on the basis of the indices described by Behrensmeyer (1975) and Badgley (1986). The spatial arrangement has been interpreted following statistical approaches (Potter and Pettijohn, 1963; Krumbein and Gayskill, 1965; Peña Sánchez de Rivera, 1987). The study of bone

modification features (mainly breakage, weathering, abrasion, corrosion and other surface marks) follows the works by Behrensmeyer (1978, 1991), Shipman (1981), Fiorillo (1991) and Alcalá Martínez (1994).

### 3.3. Taphonomic features

The variables for the bone assemblage data are shown in Fig. 5. We have essentially followed the methods described by Alcalá Martínez (1994) and Montoya (1994) for the Neogene mammalian assemblages of the Iberian Peninsula. Taphonomic features include field data such as the co-ordinates in space, orientation and dip, a record of the originally associated or articulated bones, and polarity in the fossiliferous stratum. Other features, e.g. the size, shape, weathering, abrasion, corrosion, breakage, additional bone surface marks, crust development, anatomical identification, and taxonomic classification were reassessed after the bone sample preparation in the laboratory (see Behrensmeyer, 1991; Fiorillo, 1997). Bone modification features can be defined as those that were the result of any post-mortem, prediagenetic process, which alters the morphology of a once-living bone (Fiorillo, 1991). These processes include those that are active in a fluvial system, as well as biological and physical processes (Binford, 1981; Fiorillo, 1988). Excluded are features that are the result of pathological processes that affect the living animal, or those geological processes that operate independently of those responsible for the formation of the site. Fossilization processes are also excluded from this definition (see Fiorillo, 1991).

### 3.4. Method biases

The main method biases in this work are as follows:

- Subjective sampling: excavations in the Laño quarry before 1995 were not mapped, and many taphonomic features were lost. Accordingly, most of the features discussed in this work include data from the 1995 field excavation of the L1A level.
- Modern breakage represents about 30% of the

**A**- Level.
**B**- Sample number.
**C**- Number of squares in the grid map.
**D**, **E** and **F**- Co-ordinates in space (X, Y and Z respectively) relative to a system of reference (square system).
**G**- Orientation relative to the north (after correcting the declination) and dip relative to the horizontal (after correcting the slope of the beds). Measured on long bones using a compass with clinometer.
**H**- Dimensions: D1 (largest dimension) > D2 (intermediate dimension) > D3 (smallest dimension). Measured at right angles to each other.
**I**- Size (volume) distribution: 1, less than 1 cm$^3$; 2, 1-16 cm$^3$; 3, 16-126 cm$^3$; 4, 126-1000 cm$^3$; 5, more than 1000 cm$^3$.
**J**- Age spectrum (ontogenetic stage): 1, immature (juvenile to subadult) individual; 2, mature (adult) individual; 3, indeterminate.
**K**- Weathering stage: 1, unweathered bone; 2, bone surface shows flaking associated with cracks; 3, deeper cracking and extensive flaking (weathering penetrates into internal structures).
**L**- Abrasion stage: 1, unabraded bone; 2, moderately abraded bone; 3, highly abraded, polished bone.
**M**- Corrosion (root traces due to humic acids): 1, none; 2, moderate; 3, high.
**N**- Breakage pattern: 1, complete bone; 2, bone broken during the excavation; 3, irregular transverse fracture; 4, smooth transverse fracture; 5, spiral fracture; 6, step or columnar fracture. Bones may display a combination of several types of fractures.
**O** - Number of breaks: 0, none; 1, one; 2, two; 3, three or more (splinter).
**P** - Geometric shape: 1, cubic or spherical; 2, elongated (D1>>D2, D2~D3); 3, flat (D1~D2, D2>>D3); 4, conical; 5, other.
**Q** - Iron crust development: 0, none; 1, present; 2, extensive.
**R** - Depth in the stratum (L1A): 1, upper (less than 20 cm); 2, lower (more than 20 cm).
**S** - Skeletal element: 1, cranial bone (including maxilla and lower jaw fragments); 2, maxilla with teeth *in situ*; 3, lower jaw with teeth *in situ*; 4, isolated teeth; 5, vertebra or portion of vertebral column (e.g. sacrum); 6, rib; 7, sternal bone; 8, scapula; 9, coracoid; 10, humerus; 11, ulna; 12, radius; 13, carpal bone; 14, ilium; 15, ischium; 16, pubis; 17, femur; 18, tibia; 19, fibula; 20, tarsal bone; 21, metapodial; 22, phalanx; 23, ganoid scale; 24, dermal element; 25, undetermined bone.
**T** - Anatomical position: 1, left; 2, right.
**U** - Taxon: 1, bony fish; 2, amphibian; 3, lizard; 4, snake; 5, undetermined turtle; 6, solemydid; 7, bothremydid; 8, dortokid; 9, undetermined crocodile; 10, eusuchian; 11, undetermined dinosaur; 12, theropod; 13, sauropod (titanosaurid); 14, ornithopod; 15, ankylosaur; 16, pterosaur; 17, mammal; 18, other taxon; 19, indeterminate.
**V** - Anatomical classification: Vertebral column - At., atlas; Ax., axis; Ce., cervical, Do., dorsal; Sa., sacral; Ca., caudal; Ch., chevron; Metapodial - Mc., metacarpal; Mt., metatarsal; Phalanx - Pr., proximal; Un., ungueal or distal; Turtle plate- Nu., nuchal; Py., pygal; Su., suprapygal; Ep., epiplastron; En., entoplastron; Hyo., hyoplastron; Hypo., hypoplastron; Me., mesoplastron; Xi., xiphiplastron.
**W** - Other information: R, element collected; RE, element put in plaster; NR, not collected.

Fig. 5. Model of taphonomic features recorded at Laño during the field work (mainly based on Behrensmeyer, 1991; Alcalá Martínez, 1994; Montoya, 1994).

Table 1
List and occurrences of the Laño continental vertebrates[a]

| | L2 | L1A | L1B |
|---|---|---|---|
| Osteichthyes | | | |
| Actinopterygii | | | |
| Ginglymodi | | | |
| Lepisosteiformes | | | |
| Lepisosteidae | | | |
| *Atractosteus* sp. | | Q+S | Q |
| Teleostei | | | |
| Elophomorpha? | | | |
| Phyllodontidae *incertae sedis* | | | |
| Gen. et sp. indet. | | S | |
| Palaeolabridae | | | |
| ?*Palaeolabrus* sp. | | S | |
| Amphibia | | | |
| Amphibia *incertae sedis* | | | |
| albanerpetonidae indet. | | | |
| Gen. et sp. indet. | | S | |
| Caudata | | | |
| Gen. et sp. indet. | | S | |
| Anura | | | |
| Anura indet. | | | |
| Gen. et sp. indet. | | S | |
| Discoglossidae | | | |
| Gen. et sp. indet. | | S | |
| Palaeobatrachidae | | | |
| Gen. et sp. indet. | | S | |
| Reptilia | | | |
| Chelonii | | | |
| Cryptodira | | | |
| Solemydidae | | | |
| *Solemys vermiculata* | | Q | Q |
| Pleurodira | | | |
| Pelomedusoides | | | |
| Bothremydidae | | | |
| *Polysternon atlanticum* | Q | Q | |
| ?*Elochelys* sp. | Q | | |
| Dortokidae | | | |
| *Dortoka vasconica* | | Q | Q |
| Squamata | | | |
| Lacertilia | | | |
| Lacertilia indet. | | | |
| Gen. et sp. indet A | | S | |
| Gen. et sp. indet B | | S | |
| Gen. et sp. indet C | | S | |
| Scincomorpha | | | |
| Gen. et sp. indet. | | S | |
| Iguanidae indet. | | | |
| Gen. et sp. indet. | | S | |
| Amphisbaenia (or Anguidae?) indet. | | | |
| Gen. et sp. indet. | | S | |
| Serpentes | | | |
| Madtsoidae | | | |
| *Madtsoia laurasiae* | Q | Q | Q |
| *Herensugea caristiorum* | | Q+S | |

Table 1 (*continued*)

| | L2 | L1A | L1B |
|---|---|---|---|
| Crocodylomorpha | | | |
| Eusuchia | | | |
| Alligatoroidea | | | |
| *Musturzabalsuchus buffetauti* | Q | Q+S | Q |
| Alligatoridae | | | |
| *Acynodon iberoocitanus* | | Q+S | Q |
| Eusuchia *incertae sedis* | | | |
| aff. *Allodaposuchus* sp. | | Q | |
| Mesoeucrocodylia indet. | | | |
| *Ischyrochampsa* sp. | Q | Q | |
| Dinosauria | | | |
| Saurischia | | | |
| Theropoda | | | |
| Neoceratosauria | | | |
| Gen. et sp. indet. | | Q | Q |
| Tetanurae | | | |
| Coelurosauria | | | |
| Dromaeosauridae | | | |
| Gen. et sp. indet. A | | Q+S | |
| Gen. et sp. indet. B | | Q+S | |
| Gen. et sp. indet. C | | S | |
| Ornithomimosauria | | | |
| Gen. et sp. indet. | | S | |
| Coelurosauria *incertae sedis* | | | |
| cf. *Euronychodon* sp. | | S | |
| Sauropoda | | | |
| Titanosauridae | | | |
| *Lirainosaurus astibiae* | Q | Q+S | Q |
| Ornithischia | | | |
| Ornithopoda | | | |
| Iguanodontia | | | |
| *Rhabdodon* sp. | Q | Q+S | Q |
| Hadrosauridae indet. | | S | |
| Ankylosauria | | | |
| Nodosauridae | | | |
| *Struthiosaurus* sp. | Q | Q+S | Q |
| Pterosauria | | | |
| Azhdarchidae | | | |
| cf. *Azhdarcho* sp. | | Q | Q |
| Mammalia | | | |
| Eutheria | | | |
| Proteutheria | | | |
| Ungulatomorpha | | | |
| 'Zhelestidae' | | | |
| *Lainodon orueetxebarriai* | | S | |
| *Lainodon* sp. | | S | |
| *Labes* sp. | | S | |
| 'Zhelestidae' indet. | | S | |

[a] L2, L1A and L1B are the vertebrate-bearing levels of the Laño quarry. Q indicates the specimens collected by quarrying and S those collected by screen-washing.

total sample. When the element was extensively broken, only field data (e.g. size, shape) were recorded.

- The occurrence of iron oxides on the bone surfaces (see section 4.4.8 on crust development) hides some useful features for both anatomical and taphonomic purposes. There is no evidence that the formation of the iron oxides altered the bone surface.
- The spatial arrangement does not take into account the depth in which the elements were found, that is they are represented in two-dimensions. Moreover, size disparity is not considered when the plan view distribution is made (statistical test).
- Weathering and abrasion stages are sometimes difficult to estimate. These variables were studied by the same person to reduce the introduction of any further errors as much as possible.

## 4. Results. Taphonomic features of the Laño bone assemblage

### 4.1. General observations

As mentioned above, the continental vertebrate remains from Laño have been recovered from three different horizons (Fig. 4). These accumulations are associated with ferruginous crusts, and the bones are often covered by iron oxides. The fossils are relatively well preserved but compressed because of crushing. The colour of the bones varies according to the stratum: pottery-like brown or red in L1A, ochre in L1B and ivory-like in L2. This fact also reflects lithological differences between the levels.

The Laño fossil assemblage is a multispecies accumulation of both large and small vertebrates. At least 39 species have been recognized, including actinopterygians, salamanders, frogs, lizards, snakes, amphisbaenians (?), pleurodiran and cryptodiran turtles; crocodilians, several kinds of saurischian and ornithischian dinosaurs, pterosaurs, and proteutherian mammals (Astibia et al., 1987, 1990a; Gheerbrant and Astibia, 1994; Pereda-Suberbiola et al., 1995; de Lapparent and

Murelaga, 1996; Rage, 1996; Buscalioni et al., 1997; Cavin, 1997; see Table 1). As far as is known, Laño is the most productive vertebrate locality yet reported in the Upper Cretaceous continental formations of Europe (Astibia et al., 1990a; Sigé et al., 1997).

The available data include information regarding the fossil assemblage, in-situ evidence from the site, and bone features (bone modification and census). The Laño taphonomic features are summarized in Table 2.

### 4.2. Fossil assemblage data

#### 4.2.1. Sample size

One thousand and fifty-three bones were documented in the L1A level during the 1995 field season (Fig. 6). The total set of bones recovered

Table 2
Taphonomic features of the Laño bone assemblage based on the 1995 sample from the L1A level (after Behrensmeyer, 1991)

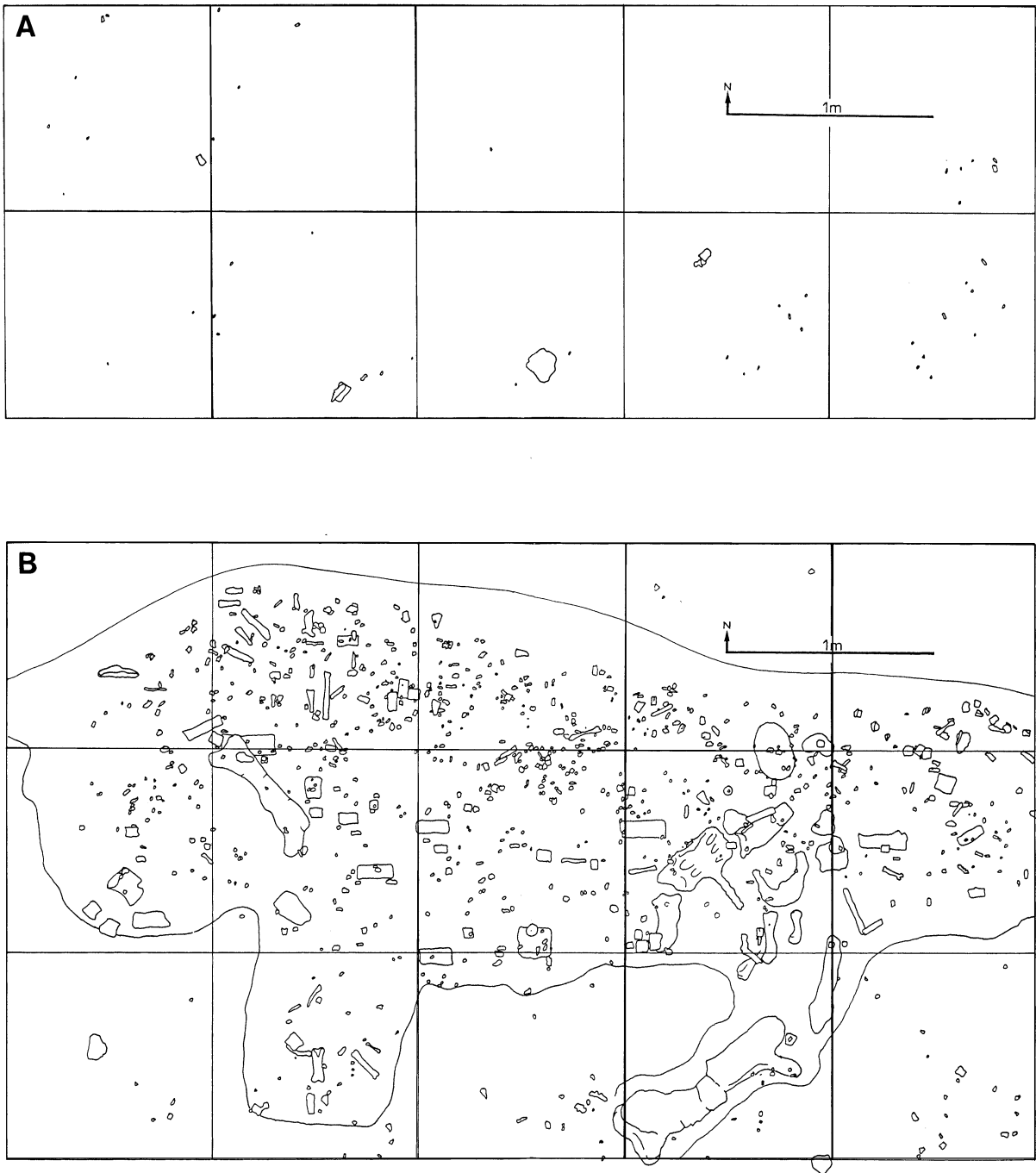| Variable | Features |
|---|---|
| **Assemblage data** | |
| Sample size | 1053 specimens |
| Number of individuals | 32 individuals |
| Number of species | 13 species |
| Relative abundance | $1-D=0.778$ (Simpson's index) |
| Body size | 70 g to 3000 kg (mode < 50 kg) |
| Age spectrum | Seven adults: one juvenile |
| Bone articulation | Articulated and associated bones < 5% |
| Skeletal parts | Sorted (dermal bones ca 71%) |
| | |
| **Quarry data** | |
| Size of accumulation | 8.25 m² |
| Spatial density | 128 bones/m² |
| Spatial arrangement | |
| In plan view | 10% long bones oriented N |
| In profile | 44% high dips (>20°) |
| Patchiness | Non-uniform distribution |
| | |
| **Bone features** | |
| Breakage | 23% complete |
| Weathering | Variable range |
| Abrasion | 40% unabraded |
| Corrosion | None |
| Other surface marks | No tooth marks, no trample marks |
| Shape of specimens | 62% flat bones |
| Size of specimens | 60% less than 5 cm³ |
| Crust development | Almost 40% bones with iron oxides |

Fig. 6. Quarry map of the Laño bone assemblage (L1A level) in 1995. (A) Superficial sample: 62 bones; (B) deep sample: 991 bones. The line represents the limits of the fully excavated area. The spatial pattern of arrangement is that of a non-uniform distribution.
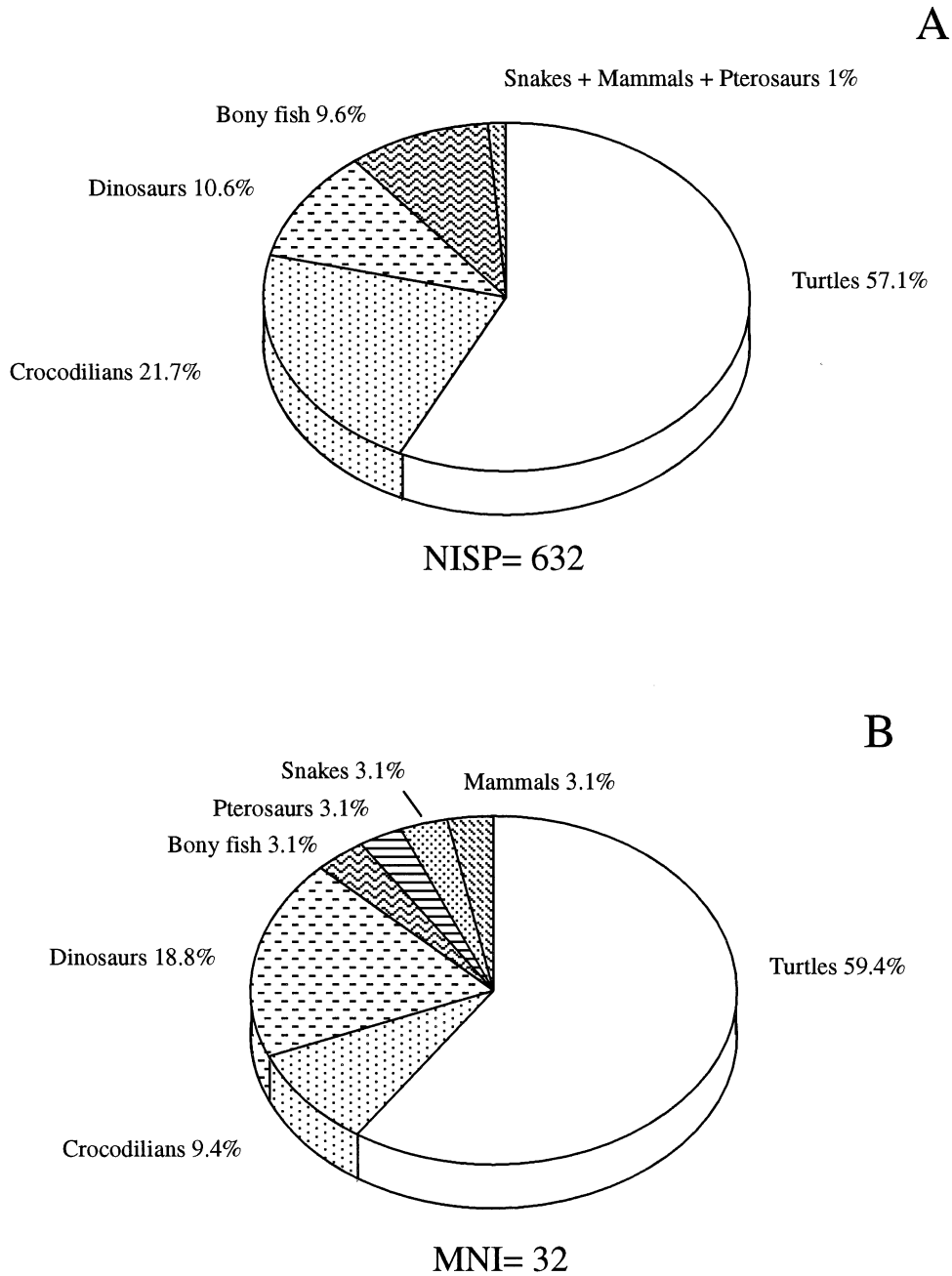
from the L1A, L1B and L2 levels during the excavations amounts to several thousand specimens (Astibia et al., 1990a).

### 4.2.2. Number of individuals

According to the 1995 field data, the number of identified specimens (NISP) in the L1A level is 632, and the minimum number of individuals (MNI) is 32 (Table 3). It should be noted that the Laño assemblage is very fragmentary, and this made the identification of the skeletal elements more difficult. As a result, the actual number of individuals in the sample is probably underestimated (see Badgley, 1986).

### 4.2.3. Number of species

A total of 13 species were recorded during the 1995 excavation in the L1A level (Table 3). Among these species, four dinosaurs, three turtles, two crocodilians, one bony fish, one pterosaur, one snake and one mammal are present. At least 39 species are represented in the Laño fossil assemblage (including the L1A, L1B and L2 levels). They are as follows: three bony fish, five amphibians, four turtles, eight squamates, four crocodilians, ten dinosaurs, one pterosaur, and four mammals (Table 1). All but one are represented

in the L1A level. The 1995 sample appears to be greatly biased in consideration of the current knowledge of the Laño site.

### 4.2.4. Taxonomic diversity

In the 1995 sample, turtles represent more than half of the identified elements (Fig. 7). The pleurodire *Dortoka* (de Lapparent and Murelaga, 1996) is by far the best represented turtle: 15 of 32 recognized individuals from the L1A level belong to this taxon (Table 3). Crocodilians are more abundant in number of specimens than dinosaurs, but the taxonomic diversity of the latter is greater. Actinopterygian fish, and especially pterosaurs, snakes and mammals, are poorly represented in the accumulation (as a whole, the latter three groups only represent 1% of the identified specimens). In the total sample, the number of amphibian individuals is larger than that of reptiles, although the latter group is dominant in number of specimens (Table 4). Palaeobatrachid amphibians, pelomedusoid turtles and alligatoroid crocodilians are the best represented vertebrates at Laño.

The relative abundance of species in Laño has been calculated from the Simpson index of diversity (Magurran, 1988) based on the 1995 data: $1 - D = 0.778$, or $1/D = 4.5$. The species richness of

Table 3
Skeletal parts and taxa represented in the Laño assemblage (L1A level, 1995 sample)

| | Croco-dilians | Turtles | Dinosauria indet. | Thero-pods | Sauro-pods | Ornitho-pods | Ankylo-saurs | Ptero-saurs | Fish | Snakes | Mam-mals | Indet. | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Skull elements | 17 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 20 |
| Maxilla or lower jaw with teeth | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Isolated teeth | 65 | 0 | 0 | 2 | 7 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 75 |
| Vertebrae | 17 | 0 | 2 | 0 | 6 | 1 | 5 | 1 | 0 | 1 | 0 | 12 | 20 |
| Ribs | 1 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 11 | 17 |
| Pectoral girdle bones | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Forelimb bones | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 4 |
| Pelvic girdle bones | 0 | 10 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 14 |
| Hind limb bones | 4 | 0 | 0 | 0 | 2 | 1 | 3 | 0 | 0 | 0 | 0 | 1 | 11 |
| Scales | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 61 | 0 | 0 | 0 | 61 |
| Osteoderms | 24 | 351 | 0 | 0 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 7 | 407 |
| Unidentified bones | 4 | 0 | 1 | 0 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 387 | 396 |
| Number of specimens | 137 | 361 | 3 | 2 | 16 | 4 | 42 | 4 | 61 | 0 | 0 | 421 | 1053 |
| Minimal number of individuals | 3 | 19 | ? | 1 | 2? | 1 | 2 | 1 | 1 | 1 | 1 | – | 32 |
| Number of species | 2 | 3 | ? | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | – | 13 |

Fig. 7. Relative abundance of Laño vertebrates in L1A from the 1995 sample. (A) Based on the number of identified specimens (NISP); (B) based on the minimum number of individuals (MNI). The assemblage is dominated by turtles. The number of crocodilian specimens is larger than that of dinosaurs, but the number of individuals of the latter group is greater.

Table 4
Relative abundance (RA) of major vertebrate groups in Laño (L1A level)[a]

|  | NSP | MNI | RA (%) |
|---|---|---|---|
| Bony fishes | 3 | 5 | 3.4 |
| Albanerpetontids | 1 | 5 | 3.4 |
| Salamanders | 1 | 4 | 2.8 |
| Frogs | 3 | 71 | 49.3 |
| Turtles | 3 | 28 | 19.4 |
| Lizards | 5 | 6 | 4.2 |
| Amphisbaenians | 1 | 1 | 0.7 |
| Snakes | 2 | 2 | 1.4 |
| Crocodilians | 4 | 5 | 3.5 |
| Dinosaurs | 10 | 12 | 8.3 |
| Pterosaurs | 1 | 1 | 0.7 |
| Mammals | 4 | 4 | 2.8 |
|  | 38 | 144 | 100 |

[a] NSP is the number of species, MNI the minimum number of individuals and RA the relative abundance (percentage of total MNI). The RA of both crocodilians and actinopterygians is probably underestimated.

the Laño sample has also been quantified using the McIntosh index ($D = 0.612$), and the Berger–Parker index ($d = 0.468$).

### 4.2.5. Body size and weight

Most of the Laño vertebrates are small in size. In the 1995 sample, nine of the 13 recorded species are smaller than 50 kg, and most of them do not exceed 1 m in length. The dominant body size is between 10 and 100 kg (Fig. 8).

In the Laño assemblage, only a third of the species are longer than 1 m (from the snout to the tip of tail). The body size of the smallest animals (amphibians and lizards) is scarcely a few cm long, and that of the largest species (a sauropod dinosaur) probably does not exceed 10 m. The body weight estimation ranges from about 15 g (tiny urodeles) to 3 tonnes (titanosaurid), but the dominant body-size mode is smaller than 1 kg (Fig. 8). The distribution model following Behrensmeyer's categories (1991) is as follows: 21 species (less than 5 kg), 11 (5–100 kg), 2 (100–500 kg), 4 (500–1000 kg) and 1 (more than 1000 kg). The macrofauna (more than 5 kg) include all the dinosaurs, most of the turtles and crocodilians (three out of four), one pterosaur and one snake.
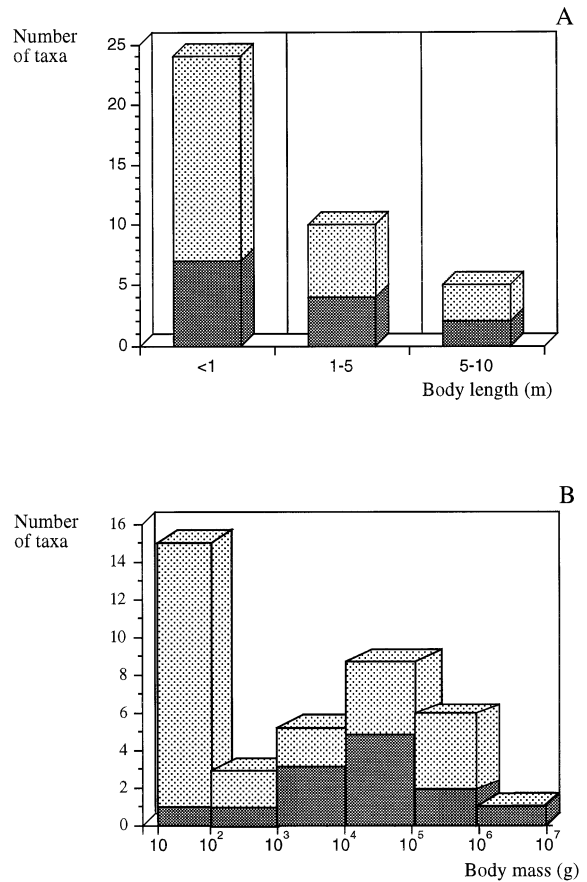


Fig. 8. Length and mass category distribution of Laño vertebrates. (A) Body length (snout-tip of tail); (B) body mass distribution. 1995 sample from the L1A level, hatched (13 species); total sample, dotted (38 species). The dominant body length is shorter than 1 m and the dominant body mass is greater than 1 kg.

### 4.2.6. Age spectrum

This parameter is much more difficult to estimate for reptiles and lower vertebrates than for mammals. As a result, a great part of the Laño sample (about 82%) is indeterminate with regard to an evaluation of ontogenetic stages. The ratio of juveniles to adults in the remainder of the bones is 1:7.

### 4.2.7. Skeletal articulation

Several states of articulation are represented in the Laño assemblage (see Behrensmeyer, 1991). Many of the bones are disarticulated and are thus
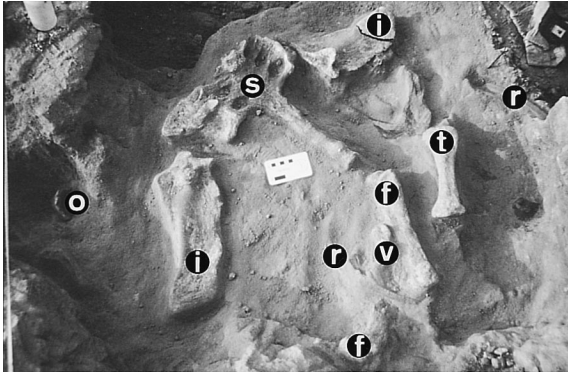
Fig. 9. Partially articulated incomplete skeleton of an ankylosaurian dinosaur recovered from the Laño L1A level during the 1995 field work. The specimen is upside down and includes a complete synsacrum (s) and portions of the pelvic girdle (i, ilium) and hindlimbs (f, femur; t, tibia), fragmentary ribs (r), dorsal vertebra (v), and osteoderms (o). The three small squares of the scale represent 1 cm each.

Murelaga, 1996). The articulated and undoubtedly associated bones recovered in L1A during the 1995 field work represent less than 5% of the assemblage.

### 4.2.8. Representation of skeletal elements

Less than two-thirds of the bones in L1A from the 1995 sample have been identified. The dermal elements (including turtle shell plates, crocodilian and ankylosaurian scutes, as well as fish scales) are, by far, the most abundant (71%) in the assemblage (Fig. 10). The isolated teeth and vertebrae each represent about 10% of the accumulation. Appendicular skeletal bones and cranial elements (including lower jaws) are very scarcely represented (less than 5%).

A representation of the skeletal parts according to taxa is shown in Table 3. Crocodilians are most completely represented as they include nearly all the anatomical categories. Turtles are essentially represented by shell remains from several regions, including both carapace and plastron. Among the dinosaurs, the ankylosaurs are the dominant group, probably because of the occurrence of a partial skeleton. Some taxa are represented by a single skeletal element. This is the case for the theropods and mammals (teeth), actinoptergygians

interpreted as accumulations of isolated and dispersed remains. The L1A level has yielded disarticulated but associated bones in spatial proximity, including skeletal elements of ankylosaurs (Fig. 9), sauropods, turtles, crocodilians and pterosaurs. Additional associated bones of turtles have been found in the L1B level. Lastly, two articulated partial shells of the most abundant turtle have been described in L1A (de Lapparent and



n= 657

Fig. 10. Relative abundance of skeletal elements in L1A based on the 1995 sample (see Table 3). The dermal elements (scales, shell plates and osteoderms) are the most abundant of the assemblage.

(scales) and snakes (vertebra). Both mammals and snakes are only represented by a single bone.

All Voorhies Groups are represented, but the bones in these groups constitute less than a third of the total identified bones. This could be because dermal bones, which are not included in the classification of Voorhies (1969), are by far the most abundant elements. Isolated teeth are the second most abundant category in the assemblage (Table 3). While isolated teeth are classically included in Voorhies Group III (Behrensmeyer, 1975, 1988), Fiorillo (1991) did not consider dinosaur teeth as belonging to Group III based on the disparity between dinosaur teeth and bones. If so, this method may also be applied to large crocodilians. Excluding the dermal bones and isolated teeth, the dominant Voorhies Group in Laño is Group I (vertebrae and ribs), which exceeds Groups II (limb bones) and III (skull bones) together. Following the method employed by Fiorillo (1991) to estimate the degree of fluvial sorting in dinosaur assemblages (ratio Voorhies Group I/Group II), 1.7 is the value obtained for Laño dinosaurs (sample equal to 27 bones). A similar value is obtained at Laño when using a tooth/vertebrae ratio. This measure, proposed by Behrensmeyer and Dechant Boaz (1980) for modern mammal ecosystems may, however, be inappropriate in dinosaur assemblages (sensu Fiorillo, 1991).

### 4.3. Quarry data

#### 4.3.1. Size of bone accumulation

Three different sites in the Laño quarry have yielded abundant continental vertebrate bones. Two of them, the so-called L1A and the overlying L1B levels, have been excavated over a surface of about 30 m² each (among which 8 m² of the L1A sample were excavated in 1995). The L2 level probably occupies an even more extensive surface, but it seems that the spatial density of elements in this level is lower than in the other levels. We estimate that the complete Laño bone accumulation is more than 100 m² in extent, but this assertion will only be confirmed by future digs.

#### 4.3.2. Spatial density

About 1053 macrofossils were recovered from the L1A level during 1995 in 8.25 m² of excavated area. This represents a concentration of about 128 specimens per square metre. If we only take into account the number of identified bones per unit area, the corresponding spatial density is about 80 per m². A detailed study of this variable by square provides estimates of 46–181 bones per m².

#### 4.3.3. Spatial pattern

In the Laño accumulation, the fossil remains are not generally juxtaposed but, at least in some areas, they are distributed closely (i.e. within cm or mm from each other) to each other. Microvertebrate remains such as fish scales or lizard pieces are mixed up with large archosaurian bones. The distribution of the bones in the L1A level is non-uniform.

Two statistical approaches have been followed to determine whether or not the horizontal distribution of the elements from two different samples is at random (Peña Sánchez de Rivera, 1987). First, the standard deviation ($\sigma$) differs considerably from the mean ($\lambda$), and this suggests that the elements are not randomly distributed. Moreover, the observed value ($\chi^2$) is considerably different from that of Pearson's ($\sigma^2$) distribution, so the null hypothesis should be rejected.

A rose diagram of the bone orientation in the L1A level (1995 sample) shows that there is a tendency for a preferentially northern orientation of the bones. A statistical test using intervals of 30°, i.e. the comparison of the standard deviation and mean (which are significantly different to each other), suggests that the bones are not randomly oriented. Both the L1A and L1B levels display a similar plan view. The preferential orientation of the bones in parallel to the paleocurrent could be explained by their disposition on the surface of a northerly prograding accretional bar.

The dip orientations are quantified as the percentage of bones dipping greater than a specified angle (e.g. 20°). Bones with subhorizontal orientations or low-angle dips seem more frequent in the L1B level than in the L1A level. In fact, about 44% of the bones of the L1A level dip more than 20° (Fig. 11).
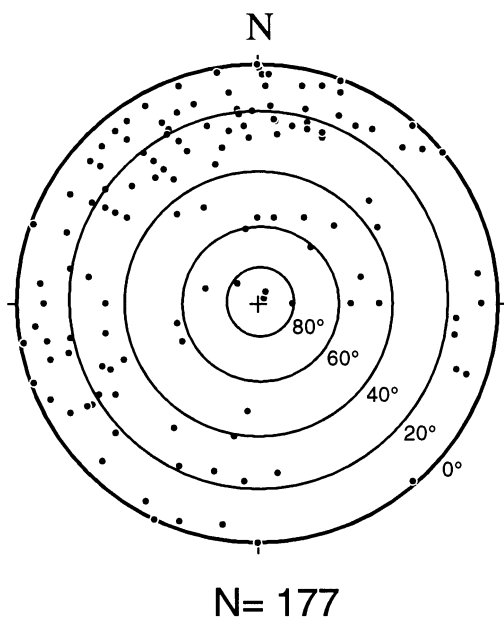
Fig. 11. Stereographic diagram of bone dip distribution in L1A (1995 sample). Note that dip is variable, with some bones being orientated at large angles to the horizontal plane.
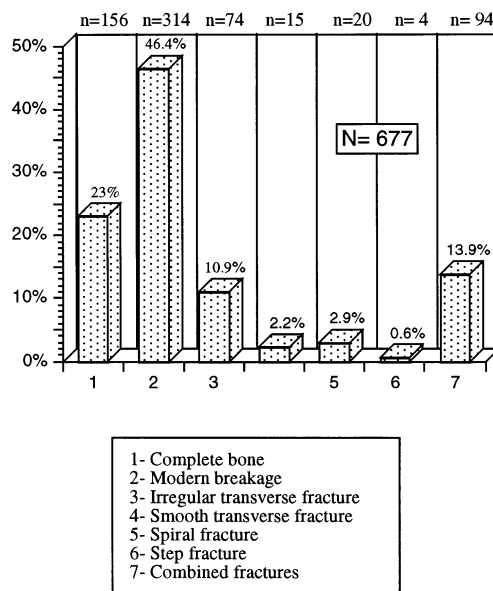


Fig. 12. Pattern of bone breakage in L1A based on the 1995 sample (categories described by Shipman, 1981; Alcalá Martínez, 1994). Three quarters of the bones are broken. The large occurrence of modern breakage is due to the fragil nature of the Laño fossils.

### 4.4. Bone features

#### 4.4.1. Breakage

Approximately three-quarters of the bones recovered from the L1A level in 1995 are broken. Most of the complete bones are isolated teeth (essentially crowns) and elements of the dermal skeleton (i.e. scutes and scales). Due to the fragile nature of the Laño fossils, almost half of the total breakage is due to handling during the excavation. The irregular transverse fracture (terminology of Alcalá Martínez, 1994; see Shipman, 1981: Fig. 5.2) is the main type of break (11%), while other types are comparatively less frequent. The occurrence of several kinds of breakage in the same specimen (combined fractures) represented a large percentage (14%) of the observed breakage (Fig. 12). The degree of breakage of dinosaur bones is larger than that of crocodilian or turtle bones (Fig. 13A). It seems that the association of both spiral and columnar fractures is more significant in dinosaurs than in turtles or crocodilians. Among turtles, there is a larger proportion of complete bones for the pleurodire *Dortoka* than for the other taxa

(Fig. 13B). Finally, two out of three bones show more than two fractures, i.e. splinters.

#### 4.4.2. Weathering

Two out of every three bones do not exhibit weathering features. Bones fully weathered, i.e. intensively cracked and flaked, only represent 1% of the accumulation. There is evidence of variable weathering according to taxon (Fig. 14A). At first sight, crocodilians and dinosaurs are comparatively less weathered than turtles. However, the turtle data appear to be biased by the high degree of weathering observed in the remains of the cryptodire *Solemys* (Fig. 14B). The pleurodiran turtles show weathering stages similar to those of the Laño archosaurians. There is also evidence of bones displaying a differential weathering pattern.

#### 4.4.3. Abrasion

Nearly 40% of the Laño bones show some evidence of abrasion. The presence of variable degrees of abrasion is also worthy of consideration.
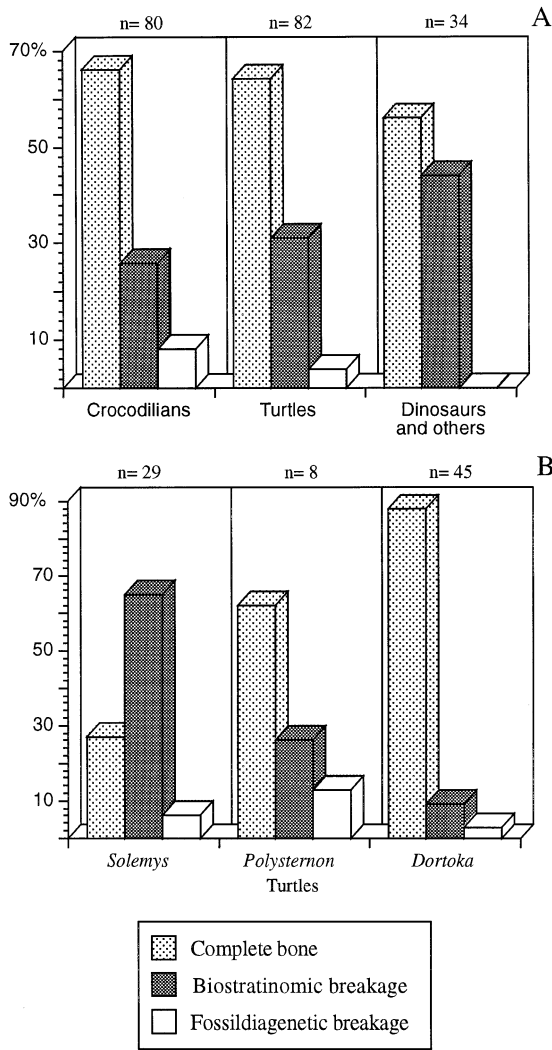
Fig. 13. Breakage distribution of bones from L1A based on the 1995 sample. (A) Among main reptile taxa; (B) within turtles. The degree of biostratinomic (pre-burial and syn-burial) breakage of dinosaur bones is larger than that of other reptiles.
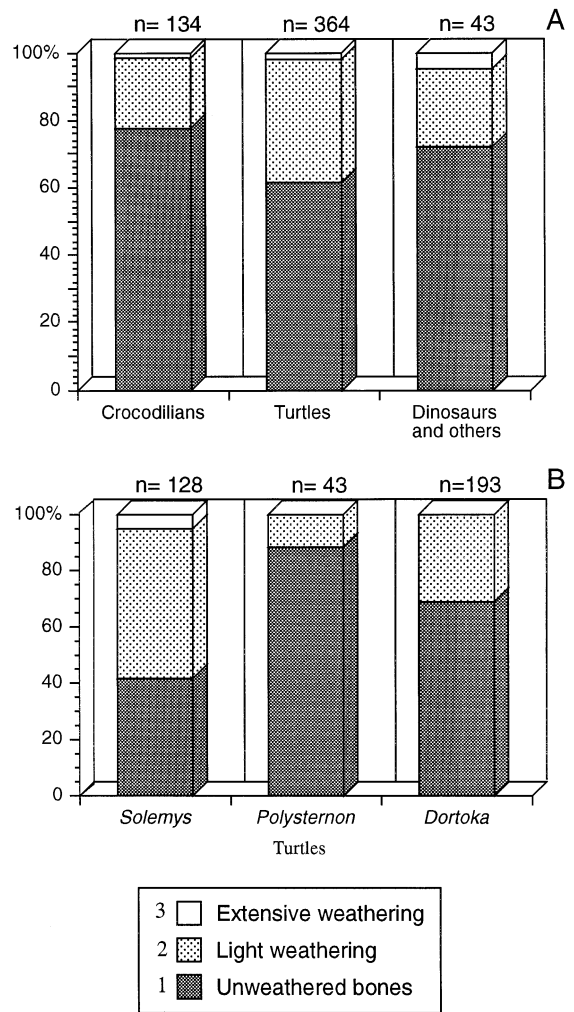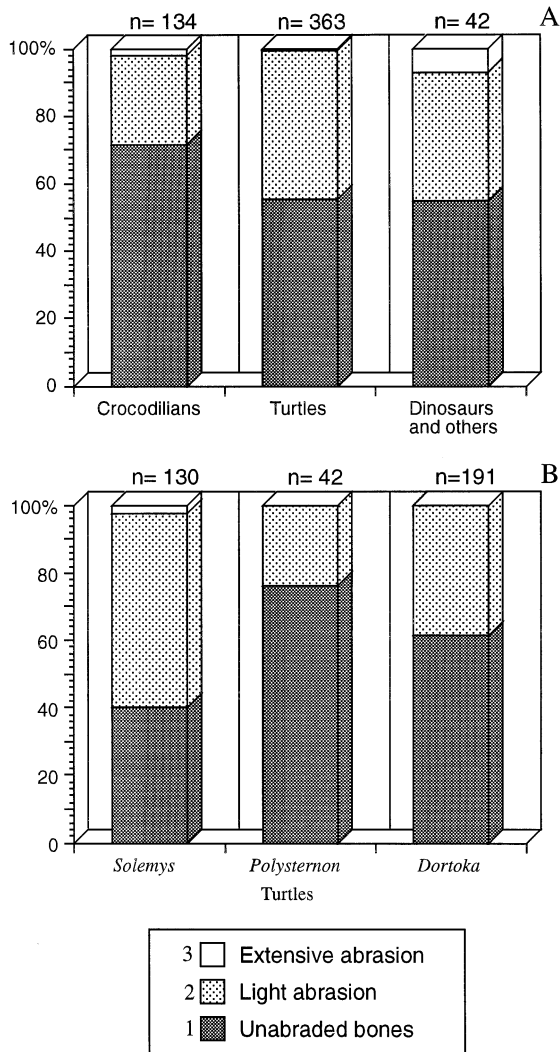


Fig. 14. Weathering stages of the bones from L1A based on the 1995 sample. (A) Among main reptile taxa; (B) within turtles. The weathering is variable according to the taxon: the fossil bones of dinosaurs and *Solemys* are more weathered than those of other groups.

Crocodilian bones are less abraded than those of dinosaurs and, apparently, turtles (Fig. 15). In fact, only the cryptodire *Solemys* shows a high degree of abrasion. The pleurodire *Polysternon* is less abraded than the other taxa, as is also the case for weathering. The higher stage of abrasion reaches 4% in dinosaurs but scarcely 1% (or less) in crocodilians and turtles.

### 4.4.4. Corrosion

There is no evidence of corrosion in the L1A level of Laño. Some bones located near, or embedded in, the upper iron crust of the L1B level show some degree of superficial corrosion as a result of the recent chemical action of plant roots.

### 4.4.5. Other surface marks

Only evidence of fungi marks on the surface of several turtle plates, including both cryptodires

Fig. 16. Fungi marks on a hyoplastron plate of turtle (*Dortoka*). These marks, present on living turtles, are indicative of an aquatic mode of life. White boxes on the scale represent 1 cm each.

group (Fig. 17). The long bones are also relatively well represented, in contrast to both equidimensional and conical elements. The dominance of flat bones is due to the large number of turtle plates, archosaurian scutes and fish ganoid scales present in the assemblage. The Flinn (1978) diagram suggests a small degree of dispersion and indicates the dominance of flat elements (Fig. 18).

### 4.4.7. Size and volume of specimens

The L1A level of Laño is characterized by the presence of a large number of small specimens.

Fig. 15. Abrasion stages of the bones from L1A based on the 1995 sample. (A) Among main reptile taxa; (B) within turtles. Dinosaur bones and *Solemys* turtle plates are comparatively more abraded than those of crocodilian and pleurodiran turtles *Dortota* and *Polysternon*.

and pleurodires, has been recognized (Fig. 16). As far as is known, there is no evidence of predator or scavenger activity at Laño, as suggested by the absence of tooth scores, gnaw marks or scratch marks on the bones.

### 4.4.6. Shape of specimens

The morphological distribution of bones shows that the flat-shaped elements are the dominant



Fig. 17. Geometric shape distribution of the bones from L1A based on the 1995 sample. The flat-shaped bones (D1~D2, D2>>D3; see Fig. 18) are predominant in the assemblage.
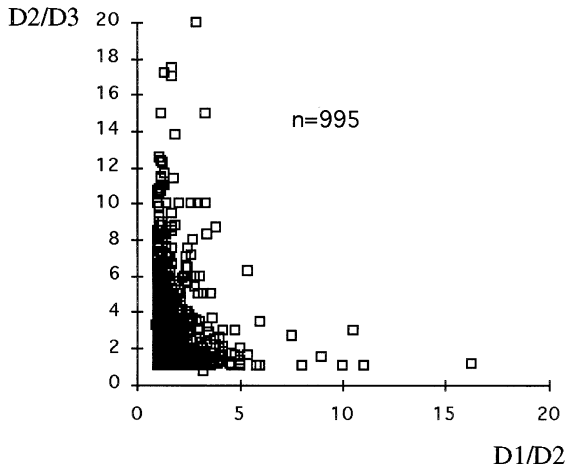
Fig. 18. Flinn diagram of the bones from L1A based on the 1995 sample. D1 is the largest dimension, D2 the intermediate dimension and D3 the smallest dimension (measured at right angles to each other). The degree of dispersion is small, and flat bones are dominant.

About 60% of the 1995 bone samples are smaller than 1 cm³ (Fig. 19). The second best represented category includes the large specimens (more than 1000 cm³). Excluding the microfossils, the typical size of the Laño specimens varies between 1 cm and 1 m approximately. Bones that are less than

10 cm in size are the dominant mode in the assemblage.

### 4.4.8. Crust development

Nearly 40% of the Laño bones are coated and impregnated with iron oxides. These oxides are present as isolated globule-shaped spots or are associated into a continuous iron surface that partially or totally hides the bone surface. The iron oxides preferentially cover the broken surfaces and the extremities of the bones (Elorza et al., 1999). These crusts are irregularly arranged, and the flat bones (dermal scutes, shell plates) are comparatively more encrusted than other types of bones. Dinosaur remains display iron oxides more frequently than those of other reptiles such as turtles and crocodilians (Fig. 20). Ankylosaurian remains, which are represented by a large number of osteoderms, display more iron oxides than those of other dinosaurs. A variable degree of crust development is also observed among turtles.

### 4.5. Microfossil features

The Laño microfossils were obtained by screen-washing of the silty sediments from the L1A level.



Fig. 19. Volume distribution of the bones from L1A based on the 1995 sample. Note that the best represented groups are the very small specimens and large specimens.
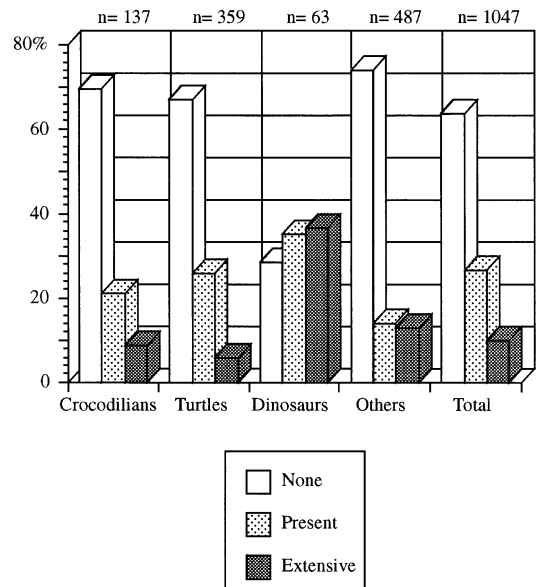


Fig. 20. Iron crust development on the bones from L1A based on the 1995 sample. Dinosaur bones are more frequently covered by iron oxides than those of other groups of vertebrates.
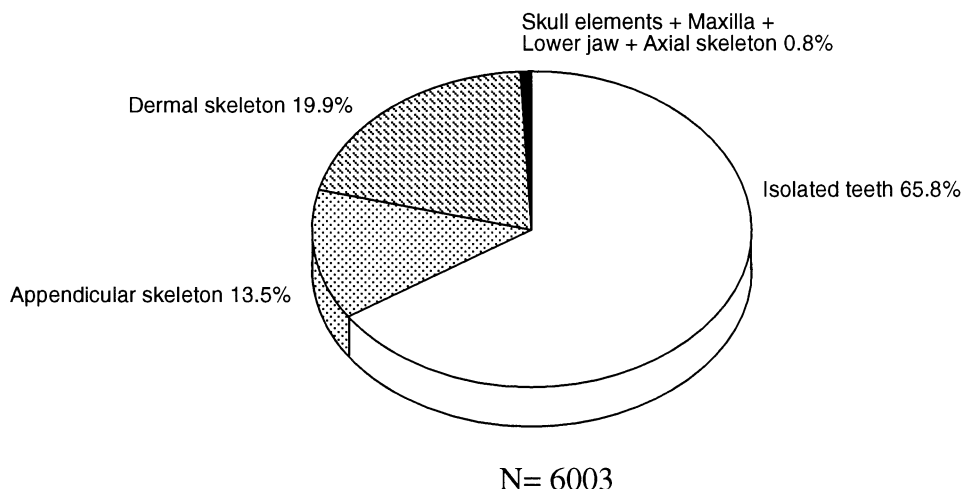
Fig. 21. Relative abundance of microfossils preserved at Laño (L1A level) based on the 1993 sample. Isolated teeth are the most common microfossils. In the sample, crocodilian remains are more abundant than those of dinosaur, turtles and other vertebrates.

In the 1993 sample, composed of about 6000 isolated bones and teeth, the most abundant elements are by far crocodilian teeth (two alligatoroid species) and fish scales (one lepisosteid species) (Fig. 21). Most of the microfossils belong to aquatic or semi-aquatic vertebrates. The turtle remains are very scarce as compared to other contemporary microfossil assemblages (Blob and Fiorillo, 1996). Terrestrial vertebrate elements such as those of dinosaurs (titanosaurid and ankylosaurian teeth) represent only 1% of the assemblage. The shape distribution shows that the cone-shaped elements (e.g. teeth) are the most common, followed by the plate-shaped (osteoderms, scales) and elongated microfossils (long bones).

### 4.6. Petrographic features

Microscopically, the crust surfaces and the iron nodules that cover the bones are composed of miscellaneous quartz crystals and are filled with iron oxides. These crystals show dissolving features due to iron oxides, as well as signs of breakage and posterior cementation by iron oxides.

The vertebrate bone mineral is well-crystallized diagenetic francolite (carbonate fluorapatite). The crystallinity degree is close to that of volcanic apatite but much greater than the poorly crystallized carbonate hydroxyapatite observed in recent mammal bones (Astibia et al., 1990b; Elorza et al., 1999).

Depending on the bone structure, several break degrees are observed. The inner and more porous tissue includes sediment (detrital quartz) and iron oxides, while in the more external region of the bones, which is composed of a more compact tissue, there is a lesser degree of breakage. In the same bone, there are some areas where the porous tissue is compressed, broken, and dislocated, whilst in other areas, the compact tissue displays only fractures that are not displaced.

Petrographic analyses using an X-ray diffractometer indicated that the iron oxides consist mainly of goethite [$FeO(OH)$]. The clay matrix is composed of about 70% illite and 30% kaolinite, whereas there is no evidence of smectite or other clay minerals. The illite crystallinity degree is about 0.55 (sensu Kübler, 1968).

## 5. Discussion

### 5.1. Biostratinomic aspects

As mentioned above, the fossil assemblage from Laño is a multispecies accumulation of both small and large vertebrates. The estimated body weights range from less than 100 g for amphibians and

mammals to about 3 tonnes for the largest dinosaur. The modal category of body size and weight is smaller than 1 m and 1 kg, respectively. The taxonomic diversity (39 species) is relatively high and is the largest known for a Late Cretaceous locality in Europe (see Sigé et al., 1997). The relative abundance of species in Laño, as quantified using a diversity index (e.g. that of Simpson), is comparable to known contemporary North American assemblages (Varricchio, 1995). Adult individuals are much more frequent than juveniles. Several states of skeletal articulation are represented, including articulated or associated specimens in close proximity, but most of the bones are disarticulated and dispersed. Dermal bones are the most common elements in the assemblage, followed by isolated teeth. All the Voorhies Groups are represented in the association.

The actual size of the Laño bone accumulation is probably much larger than that evaluated from the currently excavated area. The spatial density in the L1A level is relatively high. The bones, especially the long bones, are oriented parallel to the fluvial current, and some of them are tilted at large angles to the bedding. The bone distribution is non-uniform, with a relatively large coefficient of variation in bones per square metre. Three-quarters of the elements are broken, and two-thirds of bones are splintered. About half of the breakage is the result of combined fractures. The weathering range is variable, and the percentage of unabraded bones exceeds that of abraded bones. There is no evidence of predatory activity (e.g. tooth marks) or chemical alteration.

The Laño vertebrate assemblage occurs within channel deposits, and this has been affected by fluvial processes, as suggested by the most common long bone orientation. Biostratinomic (i.e. pre-burial and syn-burial) breakage is more common than fossildiagenetic (post-burial) fractures. This suggests that the Laño bones were mostly broken during subaereal exposition prior to transportation or after weathering, as usually happens with bones preserved in fluvial channel deposits (Behrensmeyer, 1988). The presence of a wide weathering range may be interpreted as evidence of an attritional accumulation model (Behrensmeyer, 1991). Moreover, the occurrence

of different weathering stages may reflect a complex history of subaqueous and subaerial exposure (Rogers, 1990). Abrasion is not necessarily evidence of transportation, but it may be an indicator of the intensity and/or time of interaction with the sediment (Behrensmeyer, 1991). Thus, the abrasion features observed in Laño support a complex taphonomic history of the bone assemblage. The occurrence of a large number of combined fractures is consistent with this idea.

When compared with hypothetical taphonomic examples of vertebrate accumulations (see Behrensmeyer, 1991), the Laño assemblage features are not compatible with monospecific mass accumulations due to flood. It looks like a fluvial attritional model of sorted remains of both small and large vertebrates. Nevertheless, the Laño sample differs from the hypothetical model in the presence of articulated skeletal parts, the greater representation of less-dense skeletal elements such as dermal bones and Voorhies Group I, the higher spatial density, and the greater percentage of dip. This suggests a minor influence of moving waters in Laño and the occurrence of both autochthonous and allochthonous elements mixed together in the assemblage.

The presence of two (or more) modes of fossil accumulations in Laño suggests that there are taphonomically different histories. On the one hand, the dispersed and unassociated skeletal remains were probably accumulated as sedimentary particles by the fluvial system over a large interval of time (many years?) and represent an attritional accumulation. The thickness (about 50 cm) and lithological character (sands and mudstones) of the Laño vertebrate-bearing beds suggest that the bones were probably accumulated over a period of time (and not as a result of an instantaneous event). On the other hand, the articulated and associated skeletal material includes sets of bones that were added to the bone assemblage, probably as a result of carcasses floating into the site (Fiorillo, 1991).

The features of the Laño association are intermediate between Johnson's Models II and III (Johnson, 1960). The faunal and morphological composition, fossil density, disassociation, sedimentary structure and texture in Laño are part of

Model II, which represents a gradual accumulation and burial of the remains of vertebrates living nearby or at the site of deposition. The fragmentation is in accordance with Model III, which is an assemblage composed, almost entirely, of elements transported to the site of burial. The fossil surface condition, orientation, and dispersion observed at Laño are features that are consistent with both models (Johnson, 1960).

On the basis of these data, we propose that the Laño assemblage consists of two taphonomic fractions. One fraction is interpreted here as an attritional collection of dispersed and isolated elements, while the other, which is a smaller fraction, consists of articulated or associated elements. The precise taphonomic meaning of these fractions is unclear. Nevertheless, both para-autochthonous and allochthonous elements (sensu Fernández López, 1990, 1991) are probably mixed together in the fossil association. Actinopterygian fish, amphibians, crocodilians and pleurodiran turtles are regarded as para-autochthonous elements, while the dinosaurs and probably the cryptodiran turtle, too, may be allochthonous elements. The former group includes aquatic or semi-aquatic animals, while the latter group includes terrestrial animals. Differences among turtles are interpreted as ecological preferences. This interpretation is supported by the differences observed in bone modification features between the para-autochthonous and allochthonous elements. Thus, dinosaur bones and *Solemys* plates are collectively more abraded and comparatively show a greater degree of breakage than the remaining vertebrate bones. The occurrence of bones at the death site and transported remains implies that Laño represents a mixture of vertebrates from different habitats.

The sedimentary context of the vertebrate remains and the taphonomic features of the bone association suggest that Laño is intermediate between the taphonomic modes for attritional assemblages in fluvial channels proposed by Behrensmeyer (1988), though it tends towards the channel-fill mode (Table 5). The lithology of the L1A level (mainly silt and fine sands) is comparable to that of channel-fill systems. Some of the taphonomic attributes are in accordance with this mode (e.g. variable fragmentation and abrasion; wide range of size, including microfauna; horizontal dip or at angles to a horizontal plane), but other features are characteristic of channel-lag (e.g. rare associated skeletal parts; long bones preferentially oriented with current). Thus, the Laño sample may be interpreted as a heterogeneous assemblage, which represents a number of vertebrate palaeo-communities composed of both fluvial-specific elements and specimens transported from a variety of habitats on the alluvial plain.

Table 5
Taphonomic features of the Laño bone assemblage following Behrensmeyer (1988) work for attritional vertebrate assemblages in fluvial channels

| | |
|---|---|
| ***Sedimentary context*** | |
| Large-scale | Usually in the middle to upper part of the channel |
| Small-scale | Continuous beds, not in basal lag deposits, medium to fine-grained unit |
| Lithology | Medium to fine-grained sands, clays and silts |
| Taphonomic attributes | |
| Sorting | Small sizes sorted, larger elements more common in coarse sands (L1B level) |
| Abrasion | Variable; more frequent in terrestrial vertebrate bones |
| Fragmentation | Variable; more complete in finer sediments |
| Associated skeletal parts | Rare; more common in finer sediments |
| Orientation | Long bones preferentially oriented parallel to the current |
| Dip | Horizontal or at angles to a horizontal plane |
| Body sizes | Wide range, including microfossils |
| Interpretation | |
| | Mixed assemblage, including both para-autochthonous bones deposited at death site or scarcely transported and allochthonous bones transported over a distance in the drainage basin |

## 5.2. Fossildiagenetic aspects

The faunal composition of Laño and the varied degrees of fossil preservation suggest a certain degree of spatial mixture for the L1A bone association. However, there is no evidence of a high degree of temporal mixture in this level. A low degree of taphonomic reworking (reelaboration sensu Fernández López, 1991) is likely to have taken place, based on the following fossil evidence: (1) the occurrence of articulated remains (skeletal associations) which is not consistent with reelaboration processes; (2) the low degree of smooth transverse fractures (post-burial breakage), as compared to spiral or irregular fractures, the latter occurring during the biostratinomic phase (Shipman, 1981; Alcalá and Martín Escorza, 1988); and (3) the lithological coherence between the bone filling and the sediment observed in all the thin sections.

From a petrological point of view, the vertebrate fossil bones of Laño are composed of francolite. Diagenetic processes, including the replacement of carbonate hydroxyapatite by francolite in dinosaur bones, have been described by Hubert et al. (1996). A similar phenomenon is observed in the Laño vertebrate remains, including dinosaurs, crocodilians and turtles (Elorza et al., 1999). This suggests that the diagenetic processes were homogeneous in all the fossil components.

As mentioned above, the main bone accumulations of Laño are associated with iron surfaces. These ferruginous structures were originally described as hard-grounds (Astibia et al., 1987, 1990a). The nature of these surfaces is similar to that of the iron oxides that cover the bones, as suggested by both microscopic observations and diffractogram analysis. However, the sandy and silty sediments of the L1A and L1B levels show low iron concentrations.

The bone fractures occurred before the development of the ferruginous crusts. These fractures are most often developed perpendicular to the longitudinal axis of the bones and, due to their fragil nature, were formed during the lithostatic compaction. In some cases, portions of the same bone are slightly separated from each other, and this space is filled in with iron oxides. The microscopic evidence also supports the idea that the iron oxides were formed posterior to the fractures. More than one stage of oxidation cannot be excluded.

The diagenetic processes that lead to the Laño bone features are interpreted as follows: (1) relatively rapid burial; (2) development of matrix and cement (including early cementation); (3) lithostatic compaction and fracturing of the bones and quartz grains (post-fossilization bone modification); (4) cementation of cavities and fractures (partial or total filling); (5) epidiagenesis and final fracturation (Pereda-Suberbiola et al., 1992).

The development of the crusts and globule irons could have resulted from a hydromorphic process because of seasonal variations of the phreatic water level (see Duchaufour, 1977; Meyer, 1987). In the wet season, the phreatic level becomes close to the surface, and the reducing atmosphere permits the retention of cations such as $Fe^{2+}$ dissolved in the interstitial fluids. In the dry season, intense vaporization produces a decreasing movement of the phreatic level, with the expansion of the vadose zone. The strong oxygenation generates the precipitation of the $Fe^{3+}$ as goethite or haematites. The seasonal repetition of this process permits the combination of the liberation by hydrolysis of the $Fe^{2+}$ from the phylosilicates contained in the sediment and the precipitation of iron as oxides around the fossil bones, in addition to the formation of the ferruginous crusts.

The relative percentage of illite and kaolinite suggests a climate with seasonal variations (dry and wet) of pluviosity. This model is consistent with hydromorphic processes.

## 6. Palaeoecological considerations

It is assumed that the diversity observed in the Laño fossil sample only reflects a fraction of the total diversity that was actually present in these habitats during the Late Cretaceous. The completeness of the sample based on a comparison with recent faunas ecologically similar to those represented in the Laño palaeoecosystems is difficult to assess (see methods of analysis in Estes and Berberian, 1970). Moreover, the effects due to post-mortem processes during the biostrati-

nomic phase (weathering, trampling, hydrodynamic transport, etc.) should be taken into account when reconstructing the palaeobiocenoses from the fossil association data. These biases are significantly greater in terrestrial vertebrates (especially small forms) than in animals of aquatic habitats (see Behrensmeyer et al., 1979). The occurrence of microfossils is an important source of palaeoecological data (Dodson, 1987; Brinkmann, 1990). In Laño, more than half of the species present in the L1A association have been recognized from microfossils. For example, several kinds of theropod dinosaurs are known on the basis of isolated teeth. However, it is suggested that the taphonomic (or collecting) biases may explain the absence of bird remains in the assemblage.

The Laño fossil association from the L1A level includes both aquatic (or semi-aquatic) and terrestrial vertebrates. The macrofauna are dominated by herbivorous dinosaurs such as titanosaurid sauropods (*Lirainosaurus*) and nodosaurid ankylosaurs (*Struthiosaurus*). The ornithopods (mainly *Rhabdodon*) are quite rare in the Laño assemblage. All of them constitute most of the large herbivorous biomass, apparently using different vegetation levels. *Struthiosaurus* was probably a low browsing forager (food source within 1 m above ground), while *Rhabdodon* and *Lirainosaurus* were capable of feeding on vegetation up to 2–3 m above the ground (see Weishampel, 1984). Terrestrial carnivores are represented by theropod dinosaurs of different sizes, including small dromaeosaurids and ornithomimosaurs, and a medium-sized neoceratosaurian (Pérez-Moreno et al., in prep.). Other terrestrial components of Laño are the squamates (snakes, lizards) and mammals. The small madtsoiid snake *Herensugea* was probably a fossorial or secretive form (J.-C. Rage, pers. commun.). A medium-sized azhdarchid pterosaur is the only flying vertebrate present at Laño. So far, birds have not been found in Laño.

The semi-aquatic (amphibious) components of the Laño assemblage are mainly represented by crocodilians and turtles. The occurrence of four distinct crocodilians in the L1A level is worthy of consideration. The alligatoroids *Musturzabalsuchus* and *Acynodon* are very common (Buscalioni et al., 1997), and they are regarded as para-autochthonous elements (see above). *Musturzabalsuchus* may have had alligator-like habits. The specialized dentition of *Acynodon* suggests that it fed on durophagous preys, including perhaps small turtles (although there is no direct evidence of predation in the sample). However, *Ischyrochampsa* and an *Allodaposuchus*-like eusuchian rarely occur at Laño. *Ischyrochampsa* was a huge predator that probably dwelt on land as well as in fresh water (see Vasse, 1995). Because of its large size, it was presumably capable of hunting small dinosaurs. The turtles include both cryptodiran and pleurodiran representatives (de Lapparent and Murelaga, 1996). The aquatic habits of turtles are indicated by the common presence of fungi marks on the dermal plates. The pleurodire *Dortoka* is the most common mesoreptile and was possibly a good swimmer. The cryptodire *Solemys*, the largest turtle of Laño, was presumably more terrestrial than the pleurodiran ones, as suggested by the bone modification features (higher degree of abrasion and breakage).

All the bony fish and amphibians were aquatic forms. Actinopterygians include lepisosteids (i.e. the alligator-gar *Atractosteus*) and, more rarely, teleosteans (Cavin, 1997). The amphibian fauna, largely dominated by the palaeobatrachid frogs, indicates a fresh-water environment.

The analysis of relative abundance indicates that the vertebrates with aquatic habits are dominant in the assemblage (about 80% in Table 4). The frogs account for half of the MNI, with turtles comprising about 20%. Dinosaurs are the dominant group within terrestrial vertebrates (about 8%). These data agree with a fossil association comprising an autochthonous to para-autochthonous concentration of primarily aquatic forms that inhabited freshwater environments and a minor portion of allochthonous terrestrial vertebrates.

As compared to other vertebrate localities from the Late Cretaceous of Europe, the Laño association closely resembles those of Villeveyrac and Champ-Garimond from the Campanian of Languedoc, southern France (Buffetaut et al., 1996; Sigé et al., 1997). From the 19 families of vertebrates recorded in Champ-Garimond, at least

14 are present in Laño, and no less than seven genera occur in both sites (*Atractosteus, Solemys, Polysternon, Acynodon, Musturzabalsuchus, Euronychodon, Rhabdodon*). Some of these taxa (at least eight families and four genera) also occur in Villeveyrac. The Champ-Garimond site (also called Fons 0) has been interpreted as a lacustrine environment without marine influences, while Villeveyrac is regarded as an estuarine landscape or a lagoon environment near the shoreline (Freytet, 1971; Sigé et al., 1997).

The occurrence of both pelomedusoid turtles and crocodilians in Laño indicates an intertropical, warm climate (de Lapparent and Murelaga, 1996). This interpretation agrees with the palynological assemblage found in organic matter rich beds of the alluvial system: the undergrowth of Laño was composed of ferns, gymposperm (mainly pines and cypress) and angiosperm plants, which are indicative of a humid, temperate to subtropical climate (Nuñez Betelu, pers. commun.).

## 7. Conclusions

The continental series of the Laño quarry consists of a succession of sedimentary units, including fluvial and palustrine deposits. The main fossil associations occur in an alluvial system mostly composed of sands and conglomerates with disc-shaped clasts. Most of the vertebrate bones have been found in tabular-like channel deposits. A braided river system, with channels, interchannel pools, and sandflats, is consonant with the observed sedimentary features (Astibia et al., 1990a).

The stratigraphic section of the Laño quarry shows coarse sediments (conglomerates and sands) at the bottom and fine-grained sediments (mudstones) at the top. This could be interpreted as follows: the western areas of a widespread channel represent a high-energy depositional system, while the lower-energy processes (settling) are dominant towards the east. No vertebrate fossils occur in the basal channel deposits. Most of the bones have been recovered from sandy and silty sediments towards the east.

The Laño assemblage (mainly the L1A level)

displays the following taphonomic features: size-sorting and dominance of small elements; variable degree of abrasion and fragmentation; rare articulated skeletal parts; wide range of body sizes, including microfossils; long bones somewhat preferentially oriented, and with variable dip, often at large angles to the horizontal plane. The Laño vertebrate site probably represents a mixed assemblage composed of both para-autochthonous and allochthonous elements. The precise taphonomic meaning of these fractions is unclear. The remains of aquatic (bony fish, amphibians) to semi-aquatic animals (crocodilians, turtles) were probably accumulated nearby or at the site, while those of the terrestrial vertebrates (dinosaurs, mammals) were carried over a distance in the drainage basin. Associated dinosaur bones are interpreted as a result of floating carcasses.

The fossil association of Laño lies between the extreme taphonomic modes for attritional vertebrate assemblages in fluvial channels proposed by Behrensmeyer (1988). According to the lithological features and taphonomic attributes, it tends more towards the channel-fill mode than towards the channel-lag mode. Moreover, some sedimentological features observed at Laño suggest a gradual abandonment of the channel, with occasional periods of reactivation.

The Laño association is dominated by small vertebrates with freshwater habits. The presence of pelomedusid turtles and crocodilians in Laño indicates the existence of an intertropical, warm climate.

## Acknowledgements

# References

Alcalá Martínez, L., 1994. Tafonomía. In: Macromamíferos neógenos de la fosa de Alfambra–Teruel. Inst. Est. Turolenses, Mus. Cien. Nat, Teruel, pp. 301–374.

Alcalá, L., Martin Escorza, C., 1988. Fracturación en los metápodos de *Hipparion*. Geogaceta 5, 41–44.

Anderson, J.F., Hall-Martin, A., Russell, D.A., 1985. Long-bone circumference and weight in mammals, birds and dinosaurs. J. Zool. Lond. A 207, 53–61.

Astibia, H., García-Garmilla, F., Orue-etxebarria, X., Rodriguez Lázaro, J., Buscalioni, A.D., Sanz, J.L., Jiménez-Fuentes, E., 1987. The Cretaceous–Tertiary boundary in a sector of the South limb of the Miranda–Treviño Synclinal: the first appearance of Chelonia and Archosauria in the Basque Country. Cret. Res. 8, 15–27.

Astibia, H., Buffetaut, E., Buscalioni, A.D., Cappetta, H., Corral, C., Estes, R., García-Garmilla, F., Jaeger, J.J., Jiménez Fuentes, E., Le Loeuff, J., Mazin, J.M., Orue-etxebarria, X., Pereda-Suberbiola, J., Powell, J.E., Rodriguez Lázaro, J., Sanz, J.L., Tong, H., 1990a. The fossil vertebrates from Laño (Basque Country, Spain), new evidence on the composition and affinities of the Late Cretaceous continental faunas of Europe. Terra Nova 2, 460–466.

Astibia, H., Herrero, J.M., Elorza, J.J., 1990b. An Example of Petrographic Microscopy and X-ray Diffraction Techniques as Tools in Vertebrate Taphonomic Analysis of Some Spanish Fossil Material. Com. Reun. Tafon. & Fosil, Madrid.

Baceta, J.I., 1996. El Maastrichtiense superior, Paleoceno e Ilerdiense inferior de la Región Vasco-Cantábrica: secuencias deposicionales, facies y evolución paleogeográfica. Ph.D. thesis, Univ. País Vasco, Bilbao, 372 pp.

Badgley, C., 1986. Counting individuals in mammalian fossil assemblages from fluvial environments. Palaios 1, 328–338.

Bardet, N., Corral, J.C., Pereda-Suberbiola, X., 1997. Les mosasaures (Squamata) du Crétacé supérieur du Bassin Basco-Cantabrique. Geobios, M.S. 20, 19–26.

Behrensmeyer, A.K., 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf Kenya. Bull. Mus. Comp. Zool. 146, 473–578.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4 (2), 150–162.

Behrensmeyer, A.K., 1988. Vertebrate preservation in fluvial channels. Palaeogeogr. Palaeoclimatol. Palaeoecol. 63, 183–199.

Behrensmeyer, A.K., 1991. Terrestrial vertebrate accumulations. In: Allison, P.A., Briggs, D.E.G. (Eds.), Taphonomy — Releasing the Data Locked in the Fossil Record. Plenum Press, New York, pp. 291–335.

Behrensmeyer, A.K., Western, D., Dechant Boaz, D.E., 1979. New perspectives in vertebrate paleoecology from a recent bone assemblage. Paleobiology 5 (1), 12–21.

Behrensmeyer, A.K., Dechant Boaz, D.E., 1980. The recent bones of Amboseli Park, Kenya, in relation to East African paleoecology. In: Behrensmeyer, A.K., Hill, A.P. (Eds.), Fossils in the Making. University of Chicago Press, Chicago, IL, pp. 72–92.

Behrensmeyer, A.K., Hill, A.P., 1980. Fossils in the Making. University of Chicago Press, Chicago, IL.

Belinchón, M., 1987. Estudio tafonómico y sistemático de la fauna de macromamíferos del Mioceno de Buñol (Valencia). Ph.D. thesis, Univ. Valencia, 433 pp.

Binford, L.R., 1981. Bones Ancient Men and Modern Myths. Academic Press, New York. 320 pp.

Blob, R.W., Fiorillo, A.R., 1996. The significance of vertebrate microfossil size and shape distributions for faunal abundance reconstructions: a Late Cretaceous example. Paleobiology 22 (3), 422–435.

Brinkmann, D.B., 1990. Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: evidence from vertebrate microfossil localities. Palaeogeogr. Palaeoclimatol. Palaeoecol. 78, 37–54.

Buffetaut, E., Costa, G., Le Loeuff, J., Martin, M., Rage, J.C., Valentin, X., Tong, H., 1996. An early Campanian vertebrate fauna from the Villeveyrac Basin (Hérault, southern France). N. Jb. Geol. Paläont. Mh. 1, 1–16.

Buscalioni, A.D., Ortega, F., Vasse, D., 1997. New crocodiles (Eusuchia: Alligatoroidea) from the Upper Cretaceous of southern Europe. C. R. Acad. Sci., Paris, II 325, 525–530.

Cavin, L., 1997. Les Actinoptérygiens du Turonien de Goulmima (Maroc) et l'évolution des ichthyofaunes actinoptérygiennes entre le Jurassique supérieur et le Paléocène. Ph.D. thesis, Mém. Sc. Terre Univ. P. et M. Curie, Paris, no. 9704, 218 pp.

Damuth, J., MacFadden, B.J., 1990. Body Size in Mammalian Paleobiology. Estimation and Biological Implications. Cambridge University Press, Cambridge. 397 pp.

de Lapparent, F., Murelaga, X., 1996. Une nouvelle faune de chéloniens dans le Crétacé supérieur européen. C. R. Acad. Sci. Paris II 323, 729–735.

Dodson, P., 1971. Sedimentology and taphonomy of the Oldman Formation (Campanian), Dinosaur Provincial

Park, Alberta (Canada). Palaeogeogr. Palaeoclimatol. Palaeoecol. 10, 21–74.

Dodson, P., 1987. Microfaunal studies of dinosaur paleoecology Judith River Formation of southern Alberta. In: Currie, P.J., Koster, E.H. (Eds.), Fourth Symposium of Terrestrial Ecosystems Short Papers. Occas. Pap. Tyrrell Mus. Vol. 3, 70–75.

Dodson, P., Behrensmeyer, A.K., Bakker, R.T., McIntosh, J.S., 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. Paleobiology 6 (2), 208–232.

Duchaufour, P., 1977. Manual de Edafología. Masson, Paris, 206 pp.

Efremov, J.A., 1940. Taphonomy: a new branch of Paleontology. Pan-Am. Geol. 74, 81–93.

Elorza, J.J., Astibia, H., Murelaga, X., Pereda-Suberbiola, X., 1999. Francolite as a diagenetic mineral in dinosaur and other Upper Cretaceous reptile bones (Laño, Iberian Peninsula): geochimical, microstructural and petrological features. Cret. Res. 20, 169–187.

Estes, R., Berberian, P., 1970. Paleoecology of a Late Cretaceous vertebrate community from Montana. Breviora 343, 1–35.

Fernández López, S., 1990. El significado de la autoctonía/aloctonía tafonómica. Com. Reun. Tafon. & Fosil., Madrid, pp. 115–124.

Fernández López, S., 1991. Taphonomic concepts for a theoretical biochronology. Rev. Esp. Paleontol. 6 (1), 37–49.

Fiorillo, A.R., 1988. Taphonomy of Hazard Homestead Quarry (Ogallala Group), Hitchcock County, Nebraska. Contrib. Geol. Univ. Wyoming 26 (2), 57–97.

Fiorillo, A.R., 1991. Taphonomy and depositional setting of Careless Creek Quarry (Judith River Formation), Wheatland County, Montana, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 81, 281–311.

Fiorillo, A.R., 1997. Taphonomy. In: Currie, P.J., Padian, K. (Eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego, CA, pp. 713–716.

Flinn, D., 1978. Construction and computation of three-dimensionals progressive deformations. J. Geol. Soc. Lond. 135, 291–305.

Floquet, M., 1991. La plate-forme nord-castellane au Crétacé supérieur (Espagne). Arrière-pays ibérique de la marge passive basco-cantabrique. Sédimentation et vie. Mém. géol. Univ. Dijon, Vol. 14, 925 pp. (2 vol.).

Freytet, P., 1971. Les dépôts continentaux et marins du Crétacé supérieur et des couches de passage à l'Eocène en Languedoc. Bull. BRGM, I 4, 1–54.

Gheerbrant, E., Astibia, H., 1994. Un nouveau mammifère du Maastrichtien de Laño (Pays basque espagnol). C. R. Acad. Sci. Paris, II 318, 1125–1131.

Goldstein, H., 1981. The Design and Analysis of Longitudinal Studies. Academic Press, London. 199 pp.

Gómez-Alday, J.J., García-Garmilla, F., Elorza, J.J., 1994. Evidencias de actividad diapírica sobre las unidades deposicionales del Maastrichtiense en la zona de Laño (Sur de Vitoria, Cuenca Vasco-Cantábrica). Geogaceta 16, 90–93.

Gómez-Alday, J.J., Elorza, J.J., 1998. Influencia diapírica sobre depósitos fluviales de tipo 'braided' en la cantera de Laño (Campaniense superior–Maastrichtiense superior, Cuenca Vasco-Cantábrica). Geogaceta 25.

Grigorescu, D., 1983. A stratigraphic taphonomic and paleoecologic approach to a 'forgotten land': the dinosaur-bearing deposits from the Hateg Basin (Transylvania–Romania) — Second Symposium on Mesozoic Terrestrial Ecosystems Jadwisin. Acta Palaeontol. Pol. 28, 103–121.

Hubert, J.F., Panish, P.T., Chure, D.J., Prostak, K.S., 1996. Chemistry microstructure, petrology and diagenetic model of Jurassic dinosaur bones Dinosaur National Monument. Utah J. Sedim. Res. 66 (3), 531–547.

Johnson, R.G., 1960. Models and methods for analysis of the mode of formation of fossil assemblages. Bull. Geol. Soc. Am. 71, 1075–1086.

Krumbein, W.C., Gayskill, F.A., 1965. An Introduction to Statistical Models in Geology. International Series in the Earth Sciences. McGraw-Hill, New York.

Kübler, B., 1968. Evaluation quantitative du métamorphisme par la cristallinité de l'illite. Bull. Cent. Rech. Rau-SNPA 2, 385–397.

Lucas, S.G., 1981. Dinosaur communities of the San Juan Basin: a case for lateral variations in the composition of Late Cretaceous communities. In: Lucas, S.G., Rigby Jr., J.K., Kues, B.S. (Eds.), Advances in San Juan Basin Paleontology. University of New Mexico Press, Albuquerque, NM, pp. 337–393.

Lyman, R.L., 1994. Vertebrate Taphonomy. Cambridge University Press, Cambridge. 524 pp.

Magurran, A.E., 1988. Ecological Diversity and its Measurement. Crom Helm, London. 179 pp.

Meyer, R., 1987. Paléolatérites et Paléosols. BRGM, Manuels et méthodes, 13, 163 pp.

Montoya, P., 1994. Los macromamíferos del Mioceno superior del área de Crevillente (Alicante). Ph.D. thesis, Univ. Valencia, 421 pp.

Noe-Nygaard, N., 1987. Taphonomy in archaeology with especial emphasis on man as a biasing factor. J. Danish Archaeol. 6, 7–62.

Peña Sánchez de Rivero, D., 1987. Estadística. Modelos y Métodos. Alianza Univ. Textos, Madrid. (2 vol.).

Pereda-Suberbiola, X., Corral, J.C., García-Garmilla, F., Astibia, H., 1992. Tafonomía del yacimiento de vertebrados de Laño (Cretácico superior, Cuenca Vasco-Cantábrica): datos preliminares. VIII. Jorn. Paleontol, Barcelona, pp. 119–120.

Pereda-Suberbiola, X., Astibia, H., Buffetaut, E., 1995. New remains of the armoured dinosaur *Struthiosaurus* from the Late Cretaceous of the Iberian Peninsula (Laño locality, Basque Cantabrian Basin). Bull. Soc. Géol. Fr. 166, 207–211.

Potter, P.E., Pettijohn, F.J., 1963. Paleocurrents and Basin Analysis. Springer, Berlin. 296 pp.

Rage, J.-C., 1996. Les Madtsoiidae (Reptilia, Serpentes) du Crétacé supérieur d'Europe: témoins gondwaniens d'une

dispersion transtéthysienne. C. R. Acad. Sci. Paris, II 322, 603–608.

Rogers, R.R., 1990. Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of Northwestern Montana: evidence for drought-related mortality. Palaios 5, 394–413.

Schwarcz, H.P., Hedges, R.E.M., Ivanovich, M., 1989. First International Workshop on Fossil Bone, Oxford, 18–21 July 1989. Appl. Geochem. 4 (3), 211–343.

Shipman, P., 1981. Life History of a Fossil. An Introduction to Taphonomy and Paleoecology. Harvard University Press, (Cambridge, MA).

Sigé, B., Buscalioni, A.D., Duffaud, S., Gayet, M., Orth, B., Rage, J.C., Sanz, J.L., 1997. Etat des données sur le gisement crétacé supérieur continental de Champ-Garimon (Gard, Sud de la France). Müchner Geowiss. Abh. A 34, 111–130.

Varricchio, D.J., 1995. Taphonomy of Jack's Birthday Site a diverse dinosaur bonebed from the Upper Cretaceous Two Medicine Formation of Montana. Palaeogeogr. Palaeoclimatol. Palaeoecol. 114, 297–323.

Vasse, D., 1995. *Ischyrochampsa meridionalis* n.g. n. sp., un crocodilien d'affinité gondwanienne dans le Crétacé supérieur du Sud de la France. N. Jb. Geol. Paläontol. Mon. 8, 501–512.

Voorhies, M.R., 1969. Taphonomy and Population Dynamics of an Early Pliocene Vertebrate Fauna, Knox County Nebraska Univ. Wyoming, Contr. Geol., Spec. Pap. 1., 69 pp.

Weishampel, D.B., 1984. Interactions between Mesozoic plants and vertebrates: fructifications and seed predation. N. Jb. Geol. Paläontol. Abh. 167 (2), 224–250.