Paleoichnological Outcrops of La Rioja

(Dinosaur Tracks)*

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(Dedicated to) all those people who, with their labors,

daily avenues that make La Rioja a better place.

Acknowledgements:

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* Original citation: Moratalla, J. J., Sanz, J. L. Melero, I and Jimenez, S. 1988. *Yacimientos paleoicnologocos de La Rioja. (Huellas de dinosaurios)*. Iberdrola y Gobierno de la Rioja:95pp. Translated by Martin Lockley, 2002.

Presentation (Prologue)

Paleoichnology, or the study of fossil trackways and footprints, is not a new scientific discipline. In fact it deals with a field that, after a century of neglect, has experienced an important renaissance in recent years. Numerous discoveries have come to light in different regions of the world that have contributed to the recognition of the importance of ichnites in paleobiological and paleoenvironmental research.

The authors of this volume on the fossil footprints of the La Rioja region, have not only produced a useful guide in timely fashion, but have also added an important chapter to the paleoichnological literature and to knowledge of the Early Cretaceous dinosaur communities of Europe.

The dinosaur *Iguanodon* was the first discovered, in 1822. However, despite the fact that many ichnites have been described and attributed to this genus and its relatives (Family Iguanodontidae), until very recently few have been known that are really attributable to this genus.

The outcrops of La Rioja have a special significance for various reasons. In the first place, they provide a considerable paleoichnological sample in a well-defined geological and geographical area. Secondly, because the ichnites are found at various levels across the whole area, it suggests the persistence of various groups of dinosaurs in this region for a long period in the Cretaceous. The iguanodontids responsible for the tracks were part of a large and dynamic community of dinosaurs that appears to have included other herbivores and a variety of carnivore species. Thirdly, the paleoenvironmental significance of the track-bearing strata is well interpreted, making it possible to interpret the dinosaur community as part of the Cretaceous ecosystem.

The guide is directed to scientists and general readers. It is well illustrated and researched without being excessively technical. Since the first rigorous study of fossil footprints of La Rioja appeared in the early 1970s, knowledge has increased considerably. The present volume is a fitting guide and useful synthesis of what appears to be one of the most important areas of dinosaur tracks in Europe.

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Among the many factors that have allowed mankind to occupy a privileged position in relation to other species, it has perhaps been curiosity that has allowed "him" to discover the potential of his possibilities. Curiosity for the world around, but also for the future and the past, but nothing holds sufficient explanation if we do not patiently scale the links of the chain that makes up the incredible existence of the history of the universe.

Our beloved land of La Rioja is full of revealing signs, some more recent and others more ancient, that allow the valiant researcher to patiently reconstruct each stage of our past with precise data.

Of all these signs, perhaps the most surprising (striking) for its uniqueness and antiquity would be the footprints of prehistoric animals, which dumbfound the ignorant and carry valuable information for the scientist on a stage of Earth (history) that human eyes cannot see, and which was still far from the day when the human flower would tread the blue planet.

Federico San Miguel Izarra

Director-General of Culture

Iberduero

The patronage of Iberduero in this publication is a logical consequence of the social commitment that our firm has contracted with the community whose lap its industrial activity develops. Through this commitment, Iberduero wants to foster the development (improvement) of cultural concerns, business incentives, and research projects conceived by institutions (entities) and citizens, and which reflect a society everyday more dynamic and creative.

Such a general attitude of collaboration in the publication of this paleontological memoir would be enough; but furthermore, the present study of dinosaur tracks, realized under the direction of illustrious paleontologists and moreover exhaustively describing the fossiliferous outcrops of La Rioja, is a reflection of tenacious field work, both patient and enthusiastic, by the Mineralogical and Paleontological section of Iberduero.

This group is formed of employees who add, to their everyday tasks, a scientific occupation that complements their cultural skill and optimizes their human relations; and by means of an occupation not only useful to them but also bringing to fruition realities from which all society can benefit.

Contents

Introduction

The objective of this guide which we now present is to introduce the world of paleoichnology, and in particular the field of vertebrate paleoichnology, to the public in the measure that it is possible.

A summary has been included of the historical development of this branch of paleontology, as well as a brief discussion of its development in Spain.

Also, we believe that a summary of the methods employed in the study of tracks and the information obtained by such a study is necessary. We have also included an introduction to the study of dinosaurs, in which we indicate the different types, and in particular those that inhabited the region of La Rioja and formed the great majority of tracks existing in the region.

Once we know the dinosaurs and the types of tracks discovered in La Rioja, we can understand each outcrop a little better, which we indicate on a map and briefly describe (different outlines, types of tracks, etc.).

We strove to use an accessible languages, avoiding the use of excessively technical words as much as possible. Still, at the end we include a glossary for those terms which require explanation[*]. At the same time this glossary serves as an extension of the text and includes explanatory figures on specific subjects.

This publication is generally aimed at whoever is more or less interested in the study of dinosaurs, but it may be of special interest to professors and students. If in any way it serves to make anyone become more interested in, and have a better understand of something of the world of fossils, our objective will have been accomplished.

What is Vertebrate Paleoichnology?

The paleoichnology of vertebrates is a branch of paleontology that studies footprints and the vital activity of animals of the past.

The name originates from the Greek word “icnos”, impression (from which comes also the name given to a footprint, ichnite) and “paleos”, ancient. Paleoichnology is therefore the study of fossil impressions.

The paleontologist studies two types of fossils:

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[*] “Pamine”, 3rd person voice (“a summary has been included”) has been translated as the active voice, “we have included.” The original text uses both voices. [MGL]

— direct fossils (body fossils), which are remains of a specific animal and could be bones, scales, teeth, etc.
— indirect fossils (trace fossils), products of the activity of living animals, such as ichnites (footprints), coprolites (fossil feces), gastroliths (stones swallowed by an animal to facilitate digestion or increase its density), eggs, etc….

In a broad sense, paleoichnology analyzes this second type of fossil and consequently studies primitive life through the traces of the living activity of organisms.

Brief History

In reality, the first discoveries of fossil vertebrate footprints must be lost in the obscurity of history, probably confused with tracks of birds or with the footprints of fantasy animals such as dragons or mythical creatures.

So the shepherds and farmers in the region of Enciso, Navalsaz, Préjano, etc., specifically call the dinosaur tracks discovered in the countryside footprints of Santiago's horse. Similarly, the dinosaur ichnites found on a cliff at Lagosteiros (Portugal) were incorporated into the legend of the Virgin arising from the sea mounted on a mule (Antunes, 1976). Also it has been suggested that the dinosaur ichnites discovered in the German locality of Siegfriedburg could have been the origin of the legend of Sidfrid and the dragon.

The first historical discovery for which we have a record occurred at the beginning of the 19th century, specifically in 1802, when the North American farmer Pliny Moody encountered three-toed (tridactyl) footprints of dinosaurs in South Hadley, Massachusetts. Owing to the great similarity that they showed to bird traces, but above all because dinosaurs still remained unknown, they were interpreted as the products of giant birds.

In 1828, ichnites were first discovered in Dumfrieshire, Scotland. In America, the first study was published in 1836 by E. Hitchcock, which later culminated in the first work of a monographic nature, "Ichnology of New England" in 1858. This author is the first who approached the study of ichnites seriously, to the point where the special branch of paleontology that concerns us—paleoichnology—derives. In 1836 a classification of known ichnites had already been attempted. Nevertheless, it was still thought that the Connecticut Valley imprints had been produced by birds, classified into two groups based on the morphology of the digits.

Evidently, the discovery of new ichnites, and above all the recognition of the existence of bipedal reptiles, changed this initial classification.

Meanwhile, in Europe a debate arose regarding the interpretation of the ichnogenus *Chirotherium*. The first discovery of these ichnites came to light in 1834 in Hildburghausen, Saxony. Opinions of all types were postulated, such as that they were attributable to a giant ape, or a cave bear, or a marsupial.

Chirotherium shows a pentadactyl morphology with a type of "thumb" directed towards the external side (see Fig. 1), such that its appearance resembles an inverted human hand. It is attributable to a quadrupedal animal whose skeleton has never been found with trackways or footprints that could permit its identification.

As one can see in Figure 2, the fingers in the hand of humans, and generally in all vertebrates, are numbered from interior to exterior, digit I being the thumb and therefore the little finger digit V.

The first proposed reconstruction was made by Lyell in 1842 who suggested it be attributed to a labyrinthodont (a primitive amphibian). But owing to the fact that the aforementioned exteriorly directed "thumb" was interpreted as digit I, Lyell reconstructed an animal that walked by crossing its legs (see Figure 3). In 1874, Miall suggested that the tracks of *Chirotherium* were in reality the footprints of dinosaurs. This proposal was recognized by Nopcsa in 1923, indicating that the ichnites could pertain to dinosaurs of the plateosaurid family. Nevertheless, this interpretation was quickly rejected because the foot of plateosaurids, although pentadactyl, only rested on the three central digits when walking, therefore the imprint is perceptibly different from *Chirotherium.*

The solution to the problem was suggested by Soergel in 1925. On the one hand, he proposed the idea that the "false thumb" could not be digit I, but rather in reality digit V, which would have to be extraordinarily developed with a lateral disposition. On the other hand, among available skeletal discoveries he found the taxonomic group that could have been the authors of the *Chirotherium* ichnites. They pertained to the "thecodonts", pseudosuchians from the Triassic (relatively primitive archosaurs). In this group the morphology of the foot is effectively pentadactyl, with digit V very developed and oriented laterally (see Fig. 4). Moreover, he made an anatomical reconstruction of the trackmaker from his study of these same tracks. It dealt with a quadrupedal animal that carried most of its body weight on its hind limbs and would have had a big tail in order to maintain proper balance, and moreover the presence of claws in the tracks suggested a carnivore. Its size should theoretically be about 2-5 meters (see Fig. 5).

The most important ichnological outcrops are, in general terms and following a chronological classification, as follows:

Triassic	– Connecticut Valley (Massachusetts, USA)
	– Grand Canyon National Park[*] (USA)
	– Stormberg (South Africa)
Jurassic	– Demnat Formation (Morocco)
	– Aganame Formation (Morocco)
	– Ouglagal (Morocco)
	– Glen Rose[†] (Texas, USA)
	– Purgatory River (USA)
	– Barkhausen (Germany)
	– Agades (Niger)
Cretaceous	– Weald of Hastings (England)
	– Monte Sataplia (USSR)
	– Lagosteiros (Portugal)
	– Enciso Formation (Spain)
	– Yacoraite Formation (Argentina)
	– Botuctu Formation[‡] (Brazil)
	– Queensland (Australia)
	– Agadir (Morocco)

The history of vertebrate paleoichnology can be divided into three phases on the basis of the methodology used, although this differentiation is evidently not sharp because there is an interrelation of elements between the phases.

1. descriptive phase

[*] Tracks from the Grand Canyon are Permian, not Triassic. [MGL]
[†] Not Jurassic but Cretaceous. [MGL]

2. phase of application of anatomical and biological criteria

3. phase of application of mechanical criteria

1. Descriptive phase

Encompassing the inception of paleoichnology until Soergel in 1925.

The fundamental characteristic of the study of ichnites in this first phase is specifically the description of said ichnites, using for this purpose fundamental parameters such as track length and width, interdigital angulation, digit length and width, etc. (parameters that are defined in section 7). After differentiating different types of ichnological find, this intensive descriptive activity gave way to a nomenclature based on the binomial systematics of genera and species, in this case ichnogenera and ichnospecies (parataxonomy: see glossary of terms).

2. Phase of application of anatomical and biological criteria

As we mentioned before, this stage was initiated by Soergel in 1925 with the reconstruction of the maker of Chirotherium tracks, already using eminently anatomical criteria, taking into account the theoretical structure of the skeleton, stride length, ichnite morphology, etc. Although a clear precedent existed in the reconstruction drawn by Lyell, he appeared not to have considered a fundamental detail; the minimal facility that his obsolete model presented for functioning, which produced a scarcely viable model.

Anatomical criteria had also been used (in quadrupedal dinosaurs) to tentatively calculate the length of the animal's trunk on the basis of ichnite length and stride length.

Also notorious is the study concerning paleoecological and paleoethological aspects of ichnological discoveries. So it has been possible to glimpse strategies of gregarious behavior among dinosaurs, possibly with joint defensive strategies, or the proof that sauropods—which owing to their great size were thought to be incapable of walking out of water—were probably terrestrial animals.

Also famous is the discovery of ichnites attributed to *Iguanodon* north of the Arctic Circle, and their possible relation with seasonal migrations, or perhaps a possible hibernation.

3. Phase of application of mechanical criteria

‡ Botuctu not Cretaceous but Jurassic. [MGL]

This phase was initiated by Alexander in 1976, who tried to establish a method of calculating the speed of progression of a dinosaur from the parameters of the tracks. Here, based on considerations of physical type and empirical models, a relationship was established for calculating this speed once stride length and limb height (extremity) were known (see below, section 7).

Later Demathieu (1984, 1986) developed another system, likening the movement of the limbs to a pendulum model.

Taking into account the relationships of speed, pace, and body size, Thulborn (1982) has determined the maximum theoretical velocities of diverse groups of dinosaurs.

Development in Spain

The first paleoichnological discovery for which written proof exists goes back to the discovery of *Chirotherium* footprints in Spain in 1897 in Molino de Aragón, Guadalajara (Calderon 1897); subsequently more ichnites pertaining to this ichnogenera were discovered (Longinos Navas, 1906; Gomez de Llarena, 1917). All these discoveries we restudied and analyzed by Leonardi (1959).

In regards to the specific paleoichnology of dinosaurs, the first work was not published until 1971 (Casanovas and Santafe), on tridactyl (three toed) ichnites pertaining to ornithopod and theropod dinosaurs of the Lower Cretaceous of La Rioja. These same authors described new tridactyl ichnites in the same zone (Casanovas and SantaFe 1974).

Regarding the paleoichnology of the Triassic, beside the *Chirotherium* ichnites mentioned above, another track pertaining to the same ichnogenera in Boniches, Cuenea, has been cited (Lapparent, 1966), as well as various tridactyl ichnites pertaining to diverse morphotypes in the province of Guadalajara (Demathieu et al., 1978).

Ichnites similar to these have also been reported (cited) in the Triassic of Puentenansa, Santander (Demathieu and Saiz de Omenaca, 1976).

Regarding the Jurassic, tridactyl ichnites pertaining to bipedal dinosaurs have been cited in Asturia (Garcia Ramos and Valenzuela 1977), and signs (also in Asturia) of ichnites of large size have been identified as attributable to sauropods (Sanz and Martin Escorza, in press).

The most important outcrops in our country, and logically the most studied, are found in large zone comprising (the area) between Las Sierras de Cameros Achena and Abarama (La

Rioja) across Lower Cretaceous terrain. In connection with the work of Casanovas and Santafe (1971, 1976), numerous publications have been forthcoming (Vierra and Torres, 1979; Aguirrezabala and Vierra, 1980, 1982; Aguirrezabala and Vierra, 1983; Vierra et al., 1984; Sanz et al., 1985; Aguirrezabala et al., 11985; Casanovas et al., in press; Moratalla, Sanz and Jimenez, 1998).

Various ichnological traces have also been discovered in the Lower Cretaceous of Salas de los Infantes and Regumiel de la Sierra (Burgos) 1989 (Moratalla, Sanz and Jimenez, in press), and some ichnites in Galve, Teruel (Casanovas et al., 1986).

In the majority of cases, the reported ichnites are tridactyl and pertain to bipedal dinosaurs attributed to theropods and ornithopods.

Similarly, ichnites of dinosaurs have been reported in Garunnieuse (Upper Cretaceous) of Tremp (Lérida), attributed mainly to ornithopod dinosaurs (Llompart et al., 1984).

Introduction to the Dinosaurs

The dinosaurs are a group of extinct reptiles that constituted the dominant fauna of terrestrial vertebrates during a prolonged period of time in the history of life of this planet.

Anyone who excavates a continental exposure between the Upper Triassic (approximately 200 million years ago) and the Upper Cretaceous (some 65 million years before the present) could confirm that the great majority of skeletal remains obtained pertain to dinosaurs. To what do we attribute this predominance of dinosaurs? This question is not easy to answer if we take into account that this group of reptiles made its appearance at the (same) time when the dominant faunas of terrestrial vertebrates were the advanced therapsids (Fig. 6), the immediately ancestors of our zoological class—the mammals.

Does this say that the dinosaurs were adaptively superior to the therapsids, or that some were already very close to mammalian organization? There are authors who affirm this. This adaptive superiority would consist of a notable improvement of the locomotor apparatus (limb skeleton and pectoral and pelvic girdles). In contrast to the majority of reptiles, the dinosaurs made their limbs vertical, which probably resulted in an improvement of their ability to walk (progress), moreover facilitating the support of a body mass (biomass) that on occasions could become considerable.

This characteristic of verticalization of the limbs of dinosaurs (comparable to that of mammals and birds) is considered by many researchers as an unequivocal sign that they (the dinosaurs) constitute a natural monophyletic group (that is they have a common ancestor that is not of any other animal type). We must look for the ancestors of dinosaurs among a group of archosaurs—“thecodonts” with relatively primitive characteristics. Among the forms that could have been phylogenetically closest to the origin of the dinosaurs, one finds *Lagosuchus*, a small archosaur from the Middle Triassic of Argentina. As one can see in *Lagosuchus* (Fig. 7), the oldest dinosaurs had the pelvis designated “saurischian”. In contrast to this pelvic model appeared a(nother) more advanced one (which typically defines the Ornithischia), characterized by the development of a posterior branch of the pubis (Fig. 8).

The functional (adaptive) reasons for the appearance of such a derived pelvis such as that of the ornithischian dinosaurs (convergent with that of the birds) is probably related to an improvement in the capability of movement of the femur and/or a readjustment of the center of gravity of the animal to a herbivorous mode (with a great development of the intestinal tract).

In this manner the dinosaurs divide themselves traditionally into the two groups just cited—saurischians and ornithischians. The first includes herbivorous (sauropodomorphs) and carnivorous (theropods) forms. Among the sauropodomorphs one finds the sauropods, perhaps the most popular group, of quadrupedal form with a long neck and tail (Fig. 9).

Identified traces from Enciso and Cornago may relate to this group of dinosaurs. For reasons that are not understood, sauropod tracks form a very small percentage in the known (track) record, not only in Spain, but also in the rest of the world*. The tracks of theropod dinosaurs occupy an intermediate position between sauropods and ornithopods in the track record (those of the latter are most abundant). Just as the sauropods reveal among themselves a relatively similar structural pattern, the theropods (although all carnivorous bipeds) were a very diverse group as much in size as in morphology. Some theropods such as dromaeosaurids (Fig. 10) were predators that actively pursued their prey. Others of larger size, such as *Allosaurus* (Fig. 31), are reckoned among the major predators which existed on this planet. Many of the theropod tracks of La Rioja probably pertain to forms similar to this latter genus, included in the family Megalosauridae.

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* Note.

The group of ornithischian dinosaurs is a monophyletic assemblage characterized by a very advanced modification of the cranial structure relative to the alimentary system, with a plant-eating dentition (that was) at times very effective. All have a bone in front of the dentary (predentary: see Fig. 11) and probably had cheeks similar to mammals (Fig. 11). The ornithischians include many armored quadrupedal forms (stegosaurs, Fig. 12: ankylosaurs, Fig. 13), forms with horns (ceratopsians, Fig. 14), and bipeds (ornithopods); see fig. 8. Among this group are included the majority of ichnites which appear in the outcrops of La Rioja.

One group of ornithopods, the iguanodontids, comprises the most common skeletal remains in the fossil record of Spain. The hypsilophodontids (Fig. 29) are primitive ornithopods of small size, whose skeletal remains have been discovered in Igea where they can be admired in their Municipal Museum.

Diverse aspects of the biology of dinosaurs (reproduction, feeding, behavior, physiology, etc.) have been the object of special attention in recent years and constitute an ongoing controversy. Although some authors assert that dinosaurs were viviparous, the majority are agreed that they were egg layers. Many types of eggs are known that have been mainly associated with sauropods and ornithopods. The types of egg laying are also different among various dinosaurs. Hadrosaurs are known to have constructed nests similar to those of some living crocodiles, and some authors believe that the parents remained on the nest to look after the offspring. The actual evidence indicates that at least some dinosaurs nested in colonies of a type similar to many modern sea birds.

Also one has direct and indirect evidence (aligned ichnological traces) that various types of dinosaurs had gregarious habits, that is to say many individuals congregated to form flocks or herds. It is probable that these groups formed from a specific colony, integrated by the association of related individuals.

No one knows how long a dinosaur could live, but based on the difference in size between a newborn and an adult (less than 1%) it is probable that they lived a long time, perhaps on the order of hundreds of years.

On the other hand there has been much discussion of the physiological characteristics of dinosaurs, whether they were cold blooded (ectothermic) or warm blooded (endothermic). On the basis of available evidence the majority of authors probably agree on these two observations: 1) The small and medium-sized theropods (coelurosaurs, deinonychosaurs, saurornithoidids) were probably warm blooded; 2) some forms were probably homeotherms, owing to their great body mass (sauropods) or to specific thermoregulation features (such as the plates of stegosaurs).

How is a Track Formed?

The right condition for the formation of a track is to have a substrate with a bed of fine-grained materials and great plasticity. Thus the animal leaves a complete impression that is clear in both the outline and the details such as pads, claws, etc. By contrast, a sediment that is too thick would not retain all the details.

At the same time the presence of a little layer of water is important. On the one hand, this gives a certain level of saturation which improves the cohesion between the particles of the substrate, and on the other it provides subsequent sedimentation, which will be responsible for covering the track and preserving it.

If the substrate was too dry it would not have sufficient cohesion to preserve the imprint. By contrast, if the covering layer of water is very great, its probable turbulence could distort the track to the point of erasing it.

The later sedimentation over this track plays a fundamental role, because if it produces a deposit of similar material it can mask the track in such a way that it is lost. Therefore the ideal is that the subsequent sediment that covers the impression would be of a different type. So the ichnite will appear as a discontinuity between the layers of strata, in such a way that the lower part will constitute a hollow (the hyporelief) and the upper part a filling material (the epirelief) (Fig. 15).

These conditions which we have cited must have been produced exactly in sites indicating the possible existence of ancient lakes, deltas, and coasts where the majority of tracks appear on sandstones, muds and compacted days, lacustrine limestones, etc.

Although it appears much less probable, these conditions of humidity could be produced on firm ground during rainy seasons, where it is possible to have an inundation with material that covers the tracks and allows for their preservation, if this covering up is not too abrupt.

The size of the animal is also an important factor, because an animal of great weight makes it certain that the track will be deeper, and therefore harder to erase. By contrast, smaller animals leave shallower tracks that are more easily destroyed.

Moreover, track formation is influenced by factors such as the speed of progression of the animal and the levelness of the substrate, etc.

Of What Use is the Study of Footprints?

The study of dinosaur tracks attempts to illuminate series of factors such as:

– Identification of the trackmaker

– Mode of locomotion

– Diversity of types

– Analysis of behavior (velocity, possible gregariousness, direction of movement, etc.).

Moreover, the study of the rock type containing the tracks and the (possible) fossils found in the ichnite zone can provide additional information on the paleoenvironmental conditions of the outcrop in question.

Identification of the maker of a specific track is in reality a difficult task because the shape of a track, although depending fundamentally on the morphology of the foot of the dinosaur that produced it, can be affected by a number of non-organic factors such as the following:

– Degree of compaction of the soil

– Speed

– Equilibrium in the progression of the animal

– Local irregularities, possible obstructions, etc.

– Taphonomic conditions, that is to say possible alterations produced in the interior of the rocks in which the ichnofossil remains enclosed for millions of years.

All of this carries as a consequence the fact that the same dinosaur could produce tracks that would appear to be slightly or completely different. Subsequent taphonomic processes can alter the morphology of an ichnite or erase it to a greater or lesser degree.

Still, if we were to be in front of a footprint that had not been altered by any of these factors, we would still have many difficulties in assigning it to a particular species.

Nevertheless, one can try to attribute a specific ichnite to one or another group of dinosaurs.

So it is possible on the basis of the study of footprints to have a relative idea of what type of animals populated a particular area in the past, especially where direct (body) fossils are very scarce?

A field in which the study of dinosaurs tracks can be fundamental is the analysis of behavior.

Evidently on this point, direct (body fossil) evidence (bones) give scarce information in principle, and it is specifically the branch of ichnology that has obtained or can give certain results.

So it appears clear that some groups of dinosaurs show a tendency to gregariousness, and although we do not know whether it was always the case, it appears at least that they used to travel in herds. Moreover, there are authors who have postulated that among some sauropods, the herd (flock) would have shown a specific structure, with the juvenile individuals traveling in the center of said herd and the adults on the periphery, such that it initially suggests a behavior of protecting the young.

One of the facets of locomotion that can be estimated from ichnites refers to the approximate speed that a dinosaur reveals from a particular trace. In general, the speeds obtained for dinosaurs of medium and large size correspond to the range of walking, though evidently one cannot discard the possibility of running, especially among small dinosaurs.

The study of tracks has also permitted detailed observations on the mode of progression of sauropods. At first, it used to be thought that these animals were practically incapable of walking out of the water, owing to their great size and weight. Then the discovery of certain tracks in North America allowed verification that, on the contrary, this type of dinosaur was capable of walking on firm ground.

The study of tracks can supply information regarding the predator/prey ratio, that is to say, the proportion of carnivores relative to herbivores existing in a given area. Studies done in North America indicate that the results obtained from the analysis of ichnites generally coincide with those obtained from direct (body) fossils (Lockley, 1986).

Methodological Considerations.

The study of vertebrate ichnites, and in particular those of dinosaurs, presents two aspects:

1. Study of an ichnite of individualized shape that gives us information on the morphology of the maker of said tracks.
2. Study of a track that gives us information on the mode of locomotion, speed, etc.

Study of an ichnite

In a track we can consider two types of characteristics:

a) non-metric

b) metric

a) Non-metric

This data deals with the anatomical details of the specific foot observable in the studied imprint. One has to take into account that its preservation in tracks fundamentally depends on the state of preservation of the former, and that its absence therefore does not indicate absolutely (unequivocally) that specific features did not form part of the foot that made the ichnite. In general terms, these characters are the following:

a) presence of claws in the terminal (distal) region of the digits. Their presence is of a fine and deep furrow with a sharp end.

b) presence of pads, as much in the region of the digits as in the heel.

c) presence of an interdigital membrane.

d) the shape of the heel. Although this character is difficult to define precisely, nevertheless we have established two extreme forms: 1) elongated in a posterior direction, and 2) rounded, that is to say without a clear pattern (or style).

b) Metric

Concerning the measurements that we can apply to a footprint.

The most important are the length and width (of the footprint). Length of the digit, width of the same, angles that digit II forms relative to III and this relative to digit IV. We can see these measurements schematically in Figure 16.

Study of a trackway

We give the name track or trackway to a series of consecutive footprints produced by the same animal that contains at least the impressions of the same feet.

1. bipedal trackway

2. quadrupedal trackway

The characteristic parameters of a bipedal trackway are stride, pace, trackway width, and pace angulation, which we can see schematically in Figure 7.

These characteristics are equally applicable in a quadrupedal trackway, but in addition these are others that are characteristic of this type of trackway, such as the “inter-footprint distance” (interpar*), the glenoacetabular distance, and the length of the pair (of tracks = manus and pes), which one can see in Fig. 18.

There are three methods to estimate the velocity that is revealed by a dinosaurian trackway maker: although to simplify, here we are going to explain the first of these, which was established by an English author (Alexander) in 1976. Moreover, this method is the most widely used and accepted by a large proportion of the students of this subject:

$$V = 0.25 \text{ x } g^{0.5} \text{ x } \lambda^{1.67} \text{ x } h^{-1.17}$$

where g is the acceleration due to gravity, λ is the length of the stride and h the length of the leg, considered from the ground to the hip.

The stride is a parameter that one can obtain directly from the trackway itself, but the height ‘h’ must be calculated indirectly from the length of the footprint. Alexander considers that the height of the limb (h) for a dinosaur is about four times its footprint length.

This estimation of the length evidently carries with it a high margin of error. In an effort to minimize this error we have tried to estimate this parameter (h) on the basis of known skeletons of iguanodontids as proposed by Sanz et al. (1985), which consist of the following:

1. Choose the lowest taxon possible that has a high probability of being responsible for the trackway.
2. Make a statistical analysis of the forms represented in said taxon to ultimately establish an average that relates the length of the ichnite with the (hip) height (h).

To calculate the length of the limb one has to consider two questions (factors):

a. the length of the limb is the sum of the femur, tibia, and third metatarsal, plus an increment of 9% which accounts for the additional (lengths) produced by the ankle and soft parts (Thulborn, 1982).

b. the length of the footprint has been calculated by adding an increment of 50% to the length of digit III, which refers to the anteroposterior dimension of the distal region of the metatarsal.

Regarding this hypothesis, said relationship has been verified in five species of iguanodontids: *Thescelosaurus neglectus* (Gilmore, 1913; Galton, 1974); *Tenontosaurus tilletti* (Ostrom, 1970); *Muttaburrasaurus langdoni* (Bartholomai and Molnar, 1981); *Iguanodon atherfieldensis (*Hooley, 1925); and *Iguanodon bernissartensis* (Norman, 1980) (see Table 1).

With this data a regression line has been established with the h/L relationship being (y = 3.9 x + 10.94) (See Fig. 19).

Therefore, a (given) value of x (length y of the ichnite) corresponds to a value of the length of the limb (h).

The speed following this formula (and, of course, by whatever other method used) does not have to be considered absolute, since evidently this method of calculation gives us an approximate idea of the speed, taking into account moreover that the estimate of hip height 'h' carries with it a certain percentage of error.

Types of Tracks

Among the great variety that exists in the different ichnological exposures of La Rioja we can nevertheless differentiate various basic types: on the one hand, ichnites pertaining to bipedal dinosaurs, and on the other to quadrupedal dinosaurs. Regarding the tracks of bipedal dinosaurs known to date, we can distinguish seven different types, three of which are attributed to ornithopod dinosaurs and another four to theropod dinosaurs.

Ornithopods (See Fig. 20).

OR1. It is a track of large size (average length 55-60 cm) with wide digits, a short and rounded heel. The general outline of the ichnite could be inscribed in a circle. The most typical example is the track from the exposure of La Magdalena (Préjano).

OR2. Tridactyl ichnite generally of smaller size than the former example, with wide digits and rounded ends. These tracks are more stylized than in the previous case, and instead show a greater degree of mesaxonic shape. The heel is slightly more elongated on the plantar surface, and although relatively extensive is not so ample. Sometimes there are two noticeable side indentations in front of the heel region. In one case these are clearly visible pads, as much in the digits as in the heel. For example, see the exposure of Valdeté (Préjano).

These types of tracks are attributed to ornithopods, and amongst these to the family Iguanodontidae. The well-defined difference between type OR1 in comparison to OR2 suggest that they were produced by different forms.

OR3. Tridactyl tracks of small size (average length 15-25 cm). These tracks are relatively similar to type OR2, although of smaller size. Therefore, they can be attributed in principle to ornithopods, and among these they could pertain to hypsilophodontids, pachycephalosaurs, juvenile iguanodontids, or even adult iguanodontids of small size. The problem here is that no distinguishing features exist that allow us to differentiate the imprint of a juvenile individual from an adult of small size, thus it is not possible to make a more precise identification. We can observe this type of track in the outcrops of Los Cayos B and Munilla.

Theropods (see Fig. 21)

TE1. Tridactyl ichnites of large size (approximately 50 cm in length) with long, fine digits and sharp distal ends. The general form is well shaped with a relatively narrow heel and a relatively small plantar surface. Outcrop of Valdecevillo.

TE2. Ichnites of medium size (about 30 cm long) with long, robust digits with sharp distal ends. The plantar surface is not very extensive, and the heel can be regarded as slightly elongate, although slightly rounded. Typical (examples) for example (are found) in the outcrop of El Villar and Munilla.

TE3. Tridactyl tracks of medium to large size with some digits more robust and a larger plantar surface. The size is generally less than TE1, and often clear impressions of claws are often observable at the distal ends of the digits if the preservation is good. Typical of the Los Cayos outcrop.

TE4. Ichnites of small size (15-20 cm long) with long, narrow digits with sharp distal ends. They could be attributable to coelurosaurs, although their identification is not clear owing to the fact that small ornithopods, such as hypsilophodontids with relatively narrow and elongate ungual phalanges, could theoretically leave imprints similar to this type of track. We can see this type of ichnite in the Grávalos outcrop.

This ichnological diversity suggest an indirect approach of the dinosaurs that populated the region of La Rioja during the Lower Cretaceous. Thus at least two medium to large iguanodontids appear to have existed, and possibly a form of smaller size. Moreover, type OR1 was created by a foot that still remains osteologically unknown, and which indicates a more robust and graviportal foot (adapted to support the body weight) than in *Iguanodon bernissartensis*, which moreover constitutes one of the most robust iguanodontids known to date (see Fig. 23).

Regarding the large carnosaurs, these are three clearly different types: one form with long, narrow digits responsible for a significantly elongated footprint, and another with much more robust digits. Both would be armed with powerful claws that in general have remained well impressed in the tracks, at least in those that show good preservation. The third type would be an animal of relatively small size.

The majority of tracks in La Rioja pertain to bipedal dinosaurs and there are only two rock exposures known to date, with tracks of quadrupedal dinosaurs. One of these is the Valdecevillo (Encisco) outcrop, and the other is Los Cayos (Cornago). The Valdecevillo trackway shows impressions of the hands (front feet) that are relatively small, indicating great heteropody. By contrast, the Los Cayos ichnites are all of similar size. Assuming that they could be attributable to sauropods, at first this fact seems to suggest that they were produced by different animals, perhaps a diplodocid or similar form in Valdecevillo and a camarasaurid (in the general sense) at Los Cayos.

Geological and Geographical Setting

The continental formations of the Upper Jurassic to Lower Jurassic are well represented in the region of Las Sierras de Cameros and La Demanda and their relationship with the Iberian ranges forms a structural whole practically surrounded by Tertiary deposits.

160 million years ago, a great phase of subsidence initiated in this region, probably as a result of the "Castellano Massif" tectonic elevation, which lasted for about 40 million years. This great episode of sedimentation has traditionally been divided into 5 phases that correspond to 5 lithological Groups: Tera, Onlala, Urbión, Enciso, and Olivan.

The Tera group would correspond to a complex fluvial (river) system with many relatively parallel courses that gave rise to a deltaic plain. By contrast, the Oncala group was formed by calcareous facies (limestone layers) caused by the establishment of a lake regime.

Probably a new elevation of the "Castellano Massif" gave way to a new fluvial transport with finer deposits towards the east and northeast, which formed the Urbión Group.

Next, the appearance of the "Ebro Massif" as a source of sedimentary material shifted the basin of sedimentation more towards the east, thereby creating (originating) the Enciso Group, formed by a more brackish medium. Finally a new uplift of the "Castellano Massif" was probably responsible for the new detrital deposits of the Olivan Group.

It is in the Enciso Group where dinosaur ichnites are normally found. There are ichnites that correspond to the Oncala Group (Upper Jurassic). In La Rioja the majority of exposures are found located between the basins of Rio Cidacos and Rio Alhama.

In this region the outcrops of Enciso, El Villar, Poyales, and Navalsaz have been studied. These exposures were the object of the first ichnological studies of dinosaurs published in our country (Casanovas and Santafe, 1971, 1974). Further north are found the exposures of Munilla and San Vicente, and to the east Igea. Between these we have the exposures of Cornago, Préjano, Muro de Aguas, and Grávalos.

Although there can be differences in the level of the different exposures, all appear to be included in facies of the Enciso Group. Within this (group) the different ichnological levels are still not well established, although there are outcrops situated in fetid limestones such as Valdeté and La Magdelena (Préjano), and others in calcareous sandstones. Although the precise age of this group is not completely classified, it seems probable that it is situated in the Hauterivian-Barremian (Between 130-120 million years old).

The invertebrate fossils which typically appear in these outcrops are *Unio* (clam), *Wealdenia* (snail); *Glauconia* (snail) and *Eomiodon* (clam). Also, there are isolated scales of *Lepidotes*, a holostean fish equipped with a characteristic dentition for eating molluscs (see Fig. 22).

Unio and *Wealdenia* are considered molluscs from fresh water habitats and, by contrast, the two remaining forms, *Glauconia* and *Eomiodon*, are from more brackish water. Thus, the domains of fresh and brackish water appear interrelated in various layers, which suggests the existence of an impermanent coastline, with small marine regressions and transgressions perhaps forming large floodplains where the probability of the formation and preservation of tracks may have been relatively high.

Outcrops of Munilla

The region of Munilla is rich in dinosaur tracks. They are found divided into two zones separated by the San Vicente fault. The ichnites of the first group are found situated to the north of the little pueblo of San Vicente, in varied sandstones horizons between which a stratum with a hundred tracks stands out.

The second group is found in the neighborhood of Munilla. Various strata with ichnites in different states of preservation are exposed in the outcrop, the most important being a slab of sandstone some 10 meters long and gently inclined, in which four trackways reveal different morphologies and directions of travel. The best-preserved trackway consists of 11 footprints. These ichnites are tridactyl, having been produced by a bipedal dinosaur of medium size. The digits are relatively long, although robust with relatively pointed distal ends. The heel shows lateral indentations and is relatively elongated although it ends in a rounded shape. With this morphology the tracks are included in type TE2, and are interpreted as a carnosaur. In this same stratum one observes another four trackways oriented perpendicular to the first. Two are of similar characteristics although of larger size, and two others comprise tracks of small size (which are) difficult to identify although perhaps they could be attributed to type OR4*.

Outcrops of Enciso

In Enciso and its vicinity, five outcrops with dinosaur tracks have so far been studied: Virgen del Campo, La Senoba, Valdecevillo, El Villar, and Cuesta de Andorra in Navalsaz.

The first, situated some 400 meters from the bridge over the Cidacos river, consists of a wide sandstone surface on which numerous tridactyl tracks are exposed, sufficiently separated (isolated) as to form trackways, disposed in many directions. The state of preservation is very variable, from those that are relatively well-preserved to those that are very poorly-preserved or almost imperceptible.

* Type OR4 not defined in section on track types. [MGL]

Generally the ichnites are of medium to large size and pertain to types OR2 and TE2; ornithopod dinosaurs of the family Iguanodontidae and theropod dinosaurs of the carnosaur group (see page 8).

The outcrop at Le Senoba is situated at the top of a ridge about 2.2 km from the previous outcrop. In it some ten trackways with various orientations are identified. The tracks are tridactyl and of the first three types referred to in section 8; of medium to large size (ornithopods as well as theropods) and of small size (ornithopod dinosaurs).

The outcrop of Valdecevillo is found 1.9 kilometers from the aforementioned bridge. Near the road there is a well-preserved trackway of four footprints clearly belonging to type TE1, that is a large carnosaur. This trackway is the only truly protected one in the outcrop, because it was fenced and arranged by the Iberduero section of Mineralogy and Paleontology in 1976.
Some isolated ichnites and some trackways with a variable state of preservation appear ascending on the same slab (plaque). One consists of 5 tracks of the same type and size as the fenced ones, and the other is clearly attributed to an ornithopod dinosaur.

Also a trackway produced by a quadrupedal dinosaur, probably a sauropod, is notable. The tracks corresponding to the hind feet are much larger that the fore feet.

Following the road from Enciso to Navalsaz and now at the end of El Villar one finds a new outcrop, with some 20 tracks which form three crisscrossing trackways. These ichnites have been attributed to type TE2, that is to a theropod dinosaur (Casanovas and Santa Fe, 1971).

The final outcrop is that of La Cuesta de Andorra, in front of the little village of Navalsaz. It consists of 12 tridactyl ichnites of large size (average length 68 cm and width 60 cm) with a very poor state of preservation. They are of type OR1, clearly attributable to a large ornithopod of the iguanodontid family.

Outcrops of Préjano

In the last municipality of Préjano, two outcrops with dinosaur ichnites have been discovered to date: Valdeté and La Magdelena. Their lithology corresponds to fetid lacustrine limestones.

At the outcrop of Valdeté (an area named Fuente Rinilla), one reaches Ambas Aguas by the Barrance del Soto pathway, or by the road from Muro de Aguas to Ambas Aguas. The outcrop is situated a half kilometer from the Fuente Rinilla farm yards.

One finds the outcrops in a limestone bed that reveals a trackway of 11 three-toed footprints of a bipedal dinosaur, in a good state of preservation except for ichnite number 5 (numbered in the direction of travel), which has practically disappeared owing to a fracture line on the surface of the exposure.

The tracks measure 41.5 cm long and 33 cm wide. The toes are short and rounded, and the presence of pads in both the region of the digits and the heel is noticeable. These tracks have been classified as type OR3, probably pertaining to a member of the family Iguanodontidae. The size indicates that the dinosaur would have had a leg length of approximately 1.75 meters, which corresponds to an animal 6 to 8 meters long. Its speed would have been a slow walk (4 km/hour).

Around this outcrop are another two, with isolated ichnites in very eroded and fragmented strata for which (reason) their identification and study is really problematic.

Access to La Magdalena is made from the little pueblo of Ambas Aguas, following the pathway from Barranco to Los Lobos for 2.5 km. Seven ichnites are impressed on a calcareous surface (slab). The first four are in a good state of preservation; the three others are very eroded.

They pertain to a bipedal dinosaurs and given their measurements (58.5 cm long and 60 cm wide), they indicate an animal of large size. The height of this dinosaur from the ground to the hip can be estimated at 2.4 m.

The digits are short, wide, and very rounded towards the end. One notes the presence of pads both in the digits and the heel in these tracks. Also noteworthy is the presence of a rim around the edge of the track produced by the displaced mud as a result of the pressure exerted by the foot on the wet substrate.

These ichnites (of type OR1) are attributed to a large ornithopod dinosaur in the family Iguanodontidae. Moreover, as indicated previously, they must indicate a foot much more robust and graviportal (adequate to support an increased body mass) than any of the other iguanodontids know to date. Thus if we consider *Iguanodon bernissartensis* as one of the most robust of the iguanodontids, the La Magdalena trackmaker must have had a more derived foot (see Fig. 23) with shorter and more rounded ungual phalanges, and also shorter first phalanges and short, robust metatarsals. The speed of progression at the time the impression of this trackway was made corresponds to a slow walk of 4 km/hour.

Outcrops of Muro de Aguas

There are two exposures with dinosaur tracks in the municipal district of Muro de Aguas.

The first is situated on the left of the road from Muro de Aguas to Ambas Aguas at 2.9 km from Muro.

The ichnites are exposed some 100 meters from the road and in some sandstone surfaces (slabs) in the bed of Santa Lucia arroyo. They are tridactyl and are generally found in a sorry state of preservation.

These tracks are of medium to large size (40-55 cm) long and are classified within type OR1 (iguanodontid dinosaurs).

The second outcrop is in the Chorion de Saltodero ravine. One reaches it from the pueblo of Muro by following the road which starts out from the fountain plaza for 2.5 kilometers.

The footprints appear on a large surface with an inclination of 40°. Among them are isolated tracks and two trackways that appear to cross one another; they appear very poorly preserved and one can practically not make out the digits.

Nevertheless, to the right of the surface there is an isolated track in good condition, as well as another that is found in the bed of the arroyo that runs through the aforementioned ravine. The first is 23 cm long and the second 28.5 cm.

Outcrops of Cornago.

Exposures with dinosaur ichnites have been discovered up to the present time in the Los Cayos ravine and places bordering Cornago.

Access is made by following a trail situated to the left of the main road from Arnedo to Cornago, some 21 km from this locality (Arnedo) at the foot of a big ridge from which one begins the descent to the pueblo (Cornago). The distance from the main road to outcrop A is 2.3 km and is perfectly sign-posted.

The first outcrop has been designated outcrop A because it is the most important in Los Cayos, both for the quantity of ichnites and for the quality of their preservation. It consists of a large surface of fine-grained calcareous sandstone, on the surface of which one sees abundant ripple marks, at times also visible inside these same footprints.

The stratum that covers it is found half broken off on the upper part of the outcrop, coinciding with the cut produced by the edge of the road, from which blocks break off, some of which reveal counterparts (counter molds) of tracks, that is to say the sediment that filled the holes of the tracks of this stratum.

From this same road, different beds of the (geological) section are distinguished at times making deformation or load structures visible, caused specifically by the pressure exerted on the soil by the dinosaur trampling.

A total of 26 trackways and numerous isolated footprints have so far been discovered in this exposure. Although the state of preservation of the footprints is acceptable (reasonable), there are erosional modifications to some of the trackways, and those of the left side of the surface show up (contrast) as the best preserved.

All the tracks of the outcrop are tridactyl, of a size that ranges from 30-40 cm long and 24-40 cm wide (although there are certain differences in the digit impressions). In the best preserved ichnites, impressions of claws are present in the distal portion of the digits, at times their presence is only inferred (intuited) by the geometric shape of the digits, and at times it is deduced from the remains of the sediment that covered the trackways. These digits are thick and robust, and digit III mainly shows a V-shaped outline. When the track is well preserved, the heel is slightly elongated towards the back, although rounded. At their sides there are normally indentations that are generally more pronounced on the internal (medial) region of the track. There are no appreciable digital structures such as pads. Thus they belong to type TE3, i.e. to theropod dinosaurs.

The relative similarity of all the tracks of the outcrop suggest that they were produced by similar animals, although the size and speed of progression was viable, ranging from 4-8.5 km/hour.

The majority of the of the trackways making up this exposure indicate a direction of progression towards the NW, although with a considerable degree of divergence. The trackways that do not have this orientation generally run in the opposite direction, i.e. towards the SE. Both directions of travel are relatively perpendicular to the ripple marks, i.e. towards the shore or vice versa.

Walking some 500 meters below the first outcrop one finds exposure B, which consists of a bed of 650 square meters and reveals an inclination of 37 degrees. In it there are two track levels. The lower is a sandstone, and the upper is a bluer, finer-grained sandstone which is only visible in the upper right hand part of the outcrop.

In the lower level there are around a hundred isolated footprints, oriented in all directions in a variable state of preservation. Perhaps the most interesting are those of a trackway formed by 11 footprints, although number 8 has disappeared owing to erosion. These ichnites reveal wide, rounded digits relating to type OR2 (iguanodontids).

Isolated ichnites of type OR2 crop out in the highest level, in the upper right hand of the outcrop and in some 30 m^2 of surface area, although the most interesting of this stratum is the presence of two trackways of 4 and 9 footprints of small size (20-24 cm long) which in the beginning have been attributed to ornithopods (type OR3).

The next outcrop (C) is situated relatively close to A, towards the west in one of the small gullies that flows in Los Cayos. In it there are three trackways. The first consists of 5 tracks (mean length 31.5; mean width 29.5) exposed on a grey sandstone surface. Above it is another layer of redder sandstones with unionids (bivalve molluscs) on the top, and above this level a layer of greenish limestone some 15 cm thick.

The stratum immediately above this is composed of a calcareous, grey-blue sandstone where there is another trackway of 4 footprints (mean length: 40 cm; mean width: 39 cm). The prints of these two trackways are of similar morphology to those of outcrops A and B.

Some 20 meters away one finds another trackway of 11 ichnites of subcircular morphology (mean length 37 cm, mean width 40 cm), which among them constitute the structure of a trail formed by 2 or 4 individuals. Perhaps they belong to sauropods, possibly camarasaurids, although the absence of toe structures in the ichnites does not permit this determination with a great level of confidence. Neither could we discard the possibility that they belong to an ankylosaur, or even a stegosaur, although less probably.

Towards the north of the gully, near outcrop A, are sandstones with abundant ripple marks. 7 ichnites are impressed on the stratum, forming the trail of a bipedal dinosaur. The tracks are very badly preserved with the outline often diffuse. We have named this outcrop D.

There are more isolated footprints along the length of the gully.

STRATIGRAPHY

The stratigraphic column shows a thickness of some 1,000 m, and the 28 m in which the ichnites appear in detail, distinguishing three subdivisions on the basis of lithological composition and faunal content.

Basal unit

Dark sandstones, fine-grained with a high content of mica, scarce plant remains, desiccation cracks and bioturbation, which alternate with vertically bioturbated grey mud. Both lithologies are associated together, forming sequences of decreasing grain size and energy towards the top, with cross lamination/symmetrical current ripples (Fig. 24) separated by erosional surfaces. The 5.5 m forming the unit are composed of two microsequences of diminishing stratigraphic thickness.

The sand units, and to a lesser degree the mud levels, are rich in dinosaur tracks (carnosaurs) which are aligned in the direction of movement of the animals making the footprints (tracks). One can also observe some fish scales.

Middle unit

Composed of black clays, with ferruginous nodules often of the septarian type and ripple lamination, and dark massive muds. The total thickness of the unit is 22 m with a net predominance of clays over muds[*]. These form beds of minor thickness (95-115 cm) being more common in the basal part. The separation between both lithologies is a continuous contact.

Remains of bivalves appear at the top of this unit and within the clays, and at some levels they form small black lumachels[†].

Upper unit

Dark sands of fine to medium grain, massive or with ripple lamination that alternate with grey laminated muds.

Both lithologies separated by erosional surfaces, forming sequences of decreasing size, energy and grain size.

The total thickness is some 9 m, in which one observes a predominance of muds over sands.

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[*] Fig. 24 shows this unit to be 12 m thick. [MGL]
[†] "Lumaquelas" = coquinas? [MGL]

This unit is characterized by the presence of bivalves (often with their two valves articulated) and gastropods in a good state of preservation. On occasions they form lumachels[†].

Outcrops of Igea

The ichnological outcrops of Igea cover a large region, the most interesting being those of La Canada, Las Navas, Santa Ana, and La Torre on account of their quality and ease of access.

The La Canada outcrop is found in the ravine and river bed of La Canada. Access is by the road from Igea to Cornago. Taking the road to the right, one easily arrives at the outcrop situated some 2 km from the village.

The most significant plaque (surface) of this outcrop is one of 20 meters in length, on which one observes various trackways, one of which consists of tracks. The state of preservation in this outcrop is variable.

The ichnites are tridactyl and pertain to bipedal dinosaurs of type TE2 (theropod dinosaurs).

Another interesting outcrop is that of Santa Ana, very near to the hermitage of the same name and very close to the village of Igea.

The tracks are found on a sandstone surface of limited extent. They are generally poorly impressed, although some are very deeply marked. These ichnites can be considered as pertaining to type OR2 (ornithopod dinosaurs of medium to large size).

The outcrop of La Torre is the largest in the extent and number of ichnites, all of which conform to the general outcrop of Igea. They are situated within the boundary of La Torre, to the northeast of Igea. There are up to seven levels with dinosaur tracks. Their state of preservation is very variable. The morphotypes of the tracks are equally variable, with as many tracks of theropods as these are of ornithopods.

The school boys of the region, aware of the paleontological richness of Igea, are without doubt the best guides to accompany the interested visitor.

Outcrop of Grávalos

[†] "Lumaquelas" = coquinas? [MGL]

This outcrop is situated beside the road from Arnedo to Cervera del Rió Alhama, before the 26 cm mark, past the village of Grávalos.

A total of nine trackways are observed exposed on a small sandstone surface, 7 of which are formed by tridactyl ichnites of small size (17-20 cm long and 15 wide) with fine (narrow) digits and pointed ends. They are of type TE4 (small coelurosaurian dinosaurs), although one must not discount the possibility that they also pertain to small ornithopods such as hypsilophodontids, or small carnosaurs. The trackways show a preferred direction of progression which suggests that perhaps they pertain to a small group walking gregariously.

The other two trackways appear significantly eroded and comprise tridactyl ichnites pertaining to a dinosaur of medium to large size (plaque) and following the inner bed of the arroyo; another slab occurs with tracks that appear very deteriorated, having been eroded with the bed load of hoods.

Outcrops of Cabezón de Cameros and Trevijano

The outcrops of Cabezón de Cameros, Trevijano, Vadillos, Torremuna, and bordering areas are not described in this guide because they are in the process of being cleaned, cataloged, and studied. When said studies are finished, the results that have been obtained will be published in specialized journals.

Figure 1. Schematic of left manus-pes set of *Chirotherium barthi*. i, ii, iii, iv, v: digits. Note the position of digit V situated laterally and directed towards the outside (in Sarjeant 1975).

Figure 2. Illustrations of a right human hand, in which the method of numbering fingers is shown: I: Thumb: II: Index, III: Middle (heart), IV: Ring, V: Little.

Figure 3. Reconstruction proposed by Lyell for the maker of the *Chirotherium* tracks (in Leonardi, 1959).

Figure 4. Reconstruction of the foot bones of *Ticinosuchus ferox*.

A: right manus.

B: right pes (After Krebs (1965).

Figure 5. A: reconstruction of *Ticinosuchus ferox* (in Krebs, 1965); B: theoretical reconstruction made by Soergel of the maker of the *Chirotherium* footprint (in Krebs, 1965).

Figure 6. The synapsids are a large group of reptiles characterized by having a temporal fenestra in the dorsal region (of the skull). Among these the therapsids stand out, as they had their maximum development at the end of the Paleozoic and the beginning of the Mesozoic. This group, sometimes called mammal-like reptiles, show a series of traits that related them to mammals, and are considered their ancestors. The diagram illustrates two genera of advanced therapsids relating to the group known as theriodonts, which according to some authors were active competitors with the first dinosaurs.

A: skull of *Cynognathus* in left lateral view (after Broili and Schroder in Vandebroek, 1969). One observes two characteristics typical of mammals: the differentiation in size and morphology of the teeth (heterodonty) and the tendency for the mandible to be formed of a single element, the dentary (D). Mx, Maxilla; Na, Nasal; Pr/Mx, Premaxilla; Sq, Squamosal; Vt, temporal fenestra; B, C: (on the following page) skeletal reconstruction of Th (???) (after Broom in Vandebroek, 1969).

B: left lateral view.

C: dorsal view.

Figure 7. The origin of the dinosaurs continues to be a question subject to constant debate. The Triassic of Argentina has produced relevant information in this area such as the form *Lagosuchus*, a small archosaur whose interest resides in showing a series of characteristics intermediate between the most advanced thecodonts and saurischian dinosaurs. According to Bonaparte (1975), *Lagosuchus* forms part of a radiation of thecodonts that probably gave rise to both groups of dinosaurs.

A: reconstruction of the skeleton of *Lagosuchus* in a quadrupedal stance (above) and a bipedal stance (below) (after Bonaparte, 1975).

B: life reconstruction of *Lagosuchus* (redrawn from C. Donner in V. Morell, 1987).

Figure 8. The ornithopod dinosaurs are very advanced bipedal, phytophagous (plant eaters) dinosaurs. The family Iguanodontidae constitutes a very important part of the record of the Lower Cretaceous in western Europe including Spain. Two of the best represented species are *Iguanodon mantelli* (A) and Iguanodon *bernissartensis* (B), both figures after Norman, 1980). As one can see, *I. bernissartensis* is a more robust form than *I. mantelli*. Some authors have interpreted this difference as an indication of sexual dimorphism, that is that one form represents the male and other the female of the same species of dinosaur.

Figure 9. The sauropods are quadrupedal saurischian dinosaurs characterized by long necks and tails. Although their general structure seems similar, there are differences that one can detect in the relative size of their extremities, the structure of both girdles (pelvic & pectoral), and the morphology of the vertebrae and skull. Until quite recently most authors were in agreement that, given the great mass that sauropods must have had, they would have been amphibious animals with habits similar to modern *Hippopotamus*. However, it seems very probable that in reality the sauropods were perfectly terrestrial forms. The diagram illustrates three sauropods belong to two distantly related groups: the titanosaurs (A and C) and diplodocids (B).

A: life reconstruction of *Saltasaurus*, an Argentinean titanosaur endowed with external plates (after Powell, 1986).

B: Skeletal reconstruction of *Dicraeosaurus*, from the Upper Jurassic of Tanzania.

C: reconstruction of *Neuquensaurus* ("*Titanosaurus*") *australis*, after Huene, 1929.

Figure 10. The dromaeosaurids are a group of advanced theropod dinosaurs that lived in the continents of the northern hemisphere during the Cretaceous. They constitute active predatory forms of relatively small to medium size. The figure illustrates the skull of dromaeosaurids.

A: in dorsal view (from above).

B: in right lateral view (after Colbert and Russell, 1969).

Figure 11. One of the most typical traits of the ornithischian dinosaurs is the appearance of a new bone in the lower mandible, the predentary (Pd in the drawing) which formed, together with the toothless premaxilla (Pm), a type of beak probably covered with a horny sheath (easing). This beak was used to pluck plants, which constituted its food. To complement this structure the ornithischians had cheeks similar to those of mammals[*] which facilitated the mastication of vegetation foods. These checks were inserted on (connected to) the edges of the maxilla (M) and dentary (D), and are indicated with an arrow in the illustration showing the skull of *Iguanodon* in normal left lateral view (after Norman, 1980).

Figure 12. One of the most popular groups of dinosaurs are the stegosaurs, whose remains have been discovered in North America, Europe, Asia, and Africa in sediments from the Upper Jurassic to the Lower Cretaceous. They are quadrupedal forms endowed with a peculiar dorsal alignment of skeletal structures into plates, which were originally interpreted as defenses against attacks from the large predators of the epoch. However, the majority of modern specialists appear to agree that these plates are in reality a mechanism to regulate the animal's body temperature. The given reconstruction of *Stegosaurus* is an absolute classic: after Marsh, 1896.

Figure 13. The ankylosaurs are a group of ornithischian dinosaurs characterized by their tendency to develop a strong protective dermal armor. This armor could form pieces fused into a structural continuity or also many isolated elements of diverse size and shape. Some ankylosaurs, such as *Euoplocephalus* illustrated in the figure, developed a tail club (boss) that has normally been interpreted as a defensive device used against predators. In Spain, skeletal remains of ankylosaurs have been discovered in both the Lower and Upper Cretaceous.

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[*] This claim is now disputed. [MGL]

A: life reconstruction of *Euoplocephalus*, an ankylosaur from the Upper Cretaceous of Alberta.

B: skeletal reconstruction of *Euoplocephalus* (A, B, after Carpenter, 1982).

Figure 14. The ceratopsian dinosaurs are characterized by quadrupedal forms endowed with the development of potentially defensive structures in the skull. These structures consist of the appearance of horns as much over the sides as above the orbits. Moreover, the ceratopsians rely on a type of occipital frill or collar, sometimes endowed with fine peripheral spines. The figure illustrates a reconstruction of the known genus *Triceratops*, a quadruped of some 8 meters in length which lived at the end of the Cretaceous in North America (after Ostrom and Wellnhofer, 1986).

Figure 15. Schematic illustration of the formation of an ichnite.

A: the footfall (step) of an animal.